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Shelley Nellis

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**EFFECTS OF ALTERNATIVE PREY AS A BUFFER TO PREDATION OF CHANNEL  
CATFISH (*ICTALURUS PUNCTATUS*) BY LARGEMOUTH BASS (*MICROPTERUS  
SALMOIDES*)**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science  
in Biology at Virginia Commonwealth University.

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## Table of Contents

	Page
Acknowledgements.....	ii
List of Tables.....	iv
List of Figures.....	v
Abstract.....	viii
Chapter 1: <i>A Behavioral Analysis of Bass Feeding Preference</i>	
Introduction.....	1
Methods.....	5
Results.....	8
Discussion.....	12
Tables and Figures.....	16
Chapter 2: <i>An Experimental Study of Bass Feeding Preference</i>	
Introduction.....	23
Methods.....	26
Results.....	29
Discussion.....	31
Tables and Figures.....	35
References.....	47
Appendices.....	51
Vita.....	58

## **List of Tables**

	Page
Table 1: Contingency Table for Order of Ingestion.....	16

## List of Figures

	Page
Figure 1: (A) Number of first, second, and third ingestions by largemouth bass for goldfish, bluegill, and channel catfish. (B) Scores of each prey as calculated by the selectability index....	17
Figure 2: Transitional probability diagram for order of ingestion; the probabilities indicate the likelihood that the specified prey will be ingested following ingestion of the prey at the arrow's origin. Thicker arrows indicate higher probabilities of ingestion. For example, if a bass ingests a goldfish first, there is a 68% chance that bluegill will be ingested next, and a 32% chance that catfish will be ingested next.....	18
Figure 3: (A) Mean time per trial that largemouth bass spent chasing goldfish, bluegill, and channel catfish. (B) Mean ingestion time per prey, and (C) mean ingestion time for head-first versus tail-first ingestion of channel catfish.....	19
Figure 4: Photo showing largemouth bass with channel catfish in its mouth. The catfish is upside down, and its right pectoral spine is hooked in the corner of the bass' mouth (indicated by arrow), making it impossible for the bass to swallow without repositioning the catfish.....	20
Figure 5: (A) Mean number of attempted strikes by largemouth bass of goldfish, bluegill, and channel catfish. (B) Mean percent of successful strikes per prey.....	21
Figure 6: Mean orientation time of largemouth bass toward jars with goldfish, bluegill, and channel catfish.....	22
Figure 7: Numbers of bluegill and channel catfish eaten by largemouth bass during the first net pen trial in choice and non-choice conditions. ....	35

Figure 8: Manly's $\alpha$ values calculated for the first net pen trial during which largemouth bass were presented with combinations of bluegill and channel catfish. The reference line indicates the expected preference of 50% for each prey.....	36
Figure 9: Distribution of sizes of prey eaten versus not eaten for the first trial for pens stocked with 30 catfish (A) and 30 bluegill (B) (choice), (C) pens stocked with 60 catfish (non-choice) and (D) pens stocked with 60 bluegill (non-choice).....	37
Figure 10: (A) Maximum TL, (B) mean TL and (C) mean weight of bluegill and channel catfish eaten in trial one per largemouth bass TL.....	38
Figure 11: The mean number of prey eaten by largemouth bass in the second net pen trial for pens stocked with (A) goldfish and bluegill, (B) goldfish and catfish, and (C) bluegill and catfish.....	39
Figure 12: Manly's $\alpha$ values calculated for the second net pen trial during which bass were presented with combinations of two prey; including goldfish, bluegill, and channel catfish. The reference line indicates the expected preference of 50% for each prey.....	40
Figure 13: Distribution (total length in cm) of goldfish, bluegill, and channel catfish eaten and not eaten by all largemouth bass for the second net pen trial.....	41
Figure 14: (A) Maximum TL, (B) mean TL and (C) mean weight of goldfish, bluegill, and channel catfish eaten in trial two per largemouth bass TL.....	42
Figure 15: Mean numbers of goldfish, bluegill, and channel catfish eaten by largemouth bass in the third net pen trial.....	43
Figure 16: Mean Manly's $\alpha$ values calculated for the third net pen trial during which all largemouth bass were presented with goldfish, bluegill, and channel catfish. The reference line indicates the expected preference of each prey of 33%.....	44



Figure 17: Size distributions (total length in cm) of goldfish, bluegill, and channel catfish eaten and not eaten for all largemouth bass in the third net pen trial.....	45
Figure 18: (A) Maximum TL, (B) mean TL and (C) mean weight of goldfish, bluegill, and channel catfish eaten in the third net pen trial per largemouth bass TL.....	46
Appendix I: Schematic showing arrangement of jars during the jar study.....	51
Appendix II: Arrangement of tanks for feeding trials with pumping system into adjacent pond.....	52
Appendix III: Shelter for bass constructed from peg board and PVC piping.....	53
Appendix IV: Tank with mirror used to allow observation from a short distance to minimize stress on the bass.....	54
Appendix V: Length/weight regression for bluegill; data collected by Jonathan Harris at Virginia Department of Game and Inland Fisheries.....	55
Appendix VI: Length/weight regression for channel catfish collected from aquaculture ponds at Virginia State University. The fish were purchased from a commercial supplier in Arkansas....	56
Appendix VII: Length/weight regression for goldfish measured from aquaculture-raised stocks.....	57

## **Abstract**

### **EFFECTS OF ALTERNATIVE PREY AS A BUFFER TO PREDATION OF CHANNEL CATFISH (*ICTALURUS PUNCTATUS*) BY LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*)**

By Shelley Christine Nellis, B.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2010

Director: MICHAEL L. FINE  
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Channel catfish have pectoral spines that lock to defend against gape-limited predators such as largemouth bass. Previous work indicated that spines increase survival of channel catfish exposed to bass but did not determine whether bass avoid catfish if less dangerous species are available. We presented bass with channel catfish and two alternatives, bluegill and goldfish, and compared order of ingestion, ingestion time, percent of successful strikes, and time spent chasing each prey species. We also presented the three species in a jar study that standardized position in the water column as well as in a net-pen study. The order of ingestion was suggestive of a preference for goldfish, then bluegill and finally channel catfish. Handling time was greater for channel catfish, less for bluegill, and the least for goldfish. Fewer catfish were eaten when other prey were available. Bass appear to avoid channel catfish if alternative prey is available.

## **INTRODUCTION**

Fish predators have various direct and indirect effects on populations of prey fish as predation is a key cause of mortality (Mittelbach 1986). Prey fishes have evolved various behavioral and morphological mechanisms for avoidance of predators (Kelley and Magurran 2006). Behavioral changes in prey species are induced by a predator's response to relative vulnerability of prey (Jeffries 1988). Therefore prey will adopt behaviors that reduce predation risk and increase survival (Lima and Dill 1990; Wisenden and Harter 2001; Creel et al. 2008). Similarly, morphological traits may evolve in response to predation risk (Brönmark et al. 1999; Robinson et al. 2008). Antipredator morphological traits can be important adaptations against gape-limited predators in particular (Kekäläinen et al. 2010) and may increase prey survival. For many prey species, flexibility in phenotype may allow a balance between the costs associated with defensive behaviors or morphologies, such as resource limitation, against the risk of predation (Brönmark and Miner 1992).

Channel catfish (*Ictalurus punctatus*) have pectoral spines that lock to defend against predators (Fine et al. 1997). The spine, a modified fin ray, is serrated along the posterior edge and can be locked at a right angle to the pectoral girdle (Bosher et al. 2006). An erect spine complicates ingestion by gape-limited predators such as the largemouth bass (*Micropterus salmoides*) and may discourage predation, especially if other prey are present. Bosher et al.

(2006) observed a three-fold increase in survival from bass attacks of intact channel catfish over ones with clipped spines. Bass use visual cues during strike-feeding behavior (Holt and Johnston 2009) and can learn to recognize different prey (Nyberg 1971) or aposematic bright colors in painted turtles and red-eared sliders, which cause avoidance of such prey (Britson 1998). Therefore it is possible that visual recognition of channel catfish, or other prey fish possessing anti-predation morphologies, will lead to avoidance. Boshier et al. (2006) found that bass will consume channel catfish when it is the only prey present. However, when other species are present as an alternative, bass may recognize physical differences and choose prey that lack spines and are easier to ingest. This pattern of learning has been observed in other predators, such as perch (*Perca fluviatilis*) and Northern pike (*Esox lucius*), that choose alternative prey over spined sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) (Hoogland et al. 1956).

Largemouth bass are able to discriminate prey size and tend to choose prey that are larger in apparent size or closer in proximity (Howick and O'Brien 1983). Little is known, however, about how the species of prey affects a predator's choice when prey size is consistent. In this case, physical attributes of different prey species may influence choice based on previous experience and avoidance of difficult prey in favor of easier prey. Bass will be presented with channel catfish and two other possible prey choices to determine if bass prefer fish with alternative morphologies to the spines of channel catfish. Alternative prey choices will include the bluegill sunfish (*Lepomis macrochirus*), which has a deep compressed body (Jenkins and Burkhead 1994). This morphology is interpreted as a mechanism for predator avoidance as seen in other deep-bodied species such as perch (Kekäläinen et al. 2010) and crucian carp (*Carassius carassius*) (Brönmark and Miner 1992). The third prey choice, goldfish (*Carassius auratus*), also

has a deeper body than channel catfish but is less compressed than bluegill and somewhat more cylindrical. The goldfish is soft-rayed, while bluegill have a series of small dorsal spines.

Studies have shown that deeper-bodied fish are at less risk of predation than shallow-bodied fish. Perch and carp exposed to higher predation pressure had deeper body forms than conspecifics in lakes with low predation pressure, which had a more streamlined body that is more efficient for feeding (Brönmark and Miner 1992; Kekäläinen et al. 2010). Increased and decreased spine length in sticklebacks has been related to natural selection by fish and invertebrate predators, respectively (Huntingford and Coyle 2007). Therefore predators can affect prey morphology epigenetically or through natural selection.

Moody et al. (1983) presented tiger muskellunge (*Esox masquinongy* x *E. lucius*) with two types of prey: bluegill and fathead minnow (*Pimephales promelas*), a cylindrical and soft-rayed fish. They found that the compressed body and spiny-rayed dorsal fin of bluegill, along with cover-seeking behavior, rendered the bluegill less susceptible to predation than the fathead minnow. Wahl and Stein (1988) found similar results when presenting muskellunge (*E. masquinongy*), northern pike, and tiger muskellunge with bluegill, gizzard shad (*Dorosoma cepedianum*), and fathead minnow. Predators preferred the cylindrical soft-rayed morphology of the fathead minnow to the bluegill. Differences were also seen between capture success of gizzard shad, a deep-bodied but spineless fish, and capture of bluegill, which do have spines, suggesting that body-depth and spines both function in prey preference of esocids (Wahl and Stein 1988). Other studies support this theory, as the removal of spines in sticklebacks (Hoogland et al. 1956) and channel catfish (Bosher et al. 2006) reduced the handling time for predators and decreased survival of clipped fish.

Channel catfish are more shallow-bodied than slightly depressed bluegill or goldfish, but presence of pectoral spines may allow catfish to maintain a more streamlined body form that is better suited for mobility and feeding. Pectoral spines of channel catfish (Fine et al. 1997) are much larger and less flexible than spines of bluegill (Jayne et al. 1996), which increases risk of injury to gape-limited predators. Such injuries have been documented for predatory fish (Krummrich and Heidiger 1973; Pimental et al. 1985; Ryden and Smith 2002), snakes (Burr and Stoeckel 1999) and birds (Bunkley-Williams et al. 1994; Werner et al. 2001). Glahn and Dorr (2000) found that Great Blue Heron (*Ardea herodias*), another gape-limited predator, preferred “undesirable” prey such as bluegill over channel catfish, supporting the notion that catfish spines are more dangerous than spines of bluegill.

Our goal was to determine if bass will select alternative prey over channel catfish when presented with two alternative species, all of relatively similar sizes. The somewhat cylindrical, soft-rayed goldfish seems the most likely choice. I hypothesize that bluegill, even with a morphology demonstrated to deter predation, will be preferred over channel catfish. Preference will be determined by comparing order of ingestion, ingestion time, percent of successful strikes, and time spent by the bass chasing each of the three prey species. As a top piscivore in North American freshwater and a central game fish (Garcia-Berthou 2002), it is important to determine feeding preferences of largemouth bass to assess their impacts on prey populations both in the wild and in fisheries and aquaculture.

## METHODS

**FEEDING TRIALS:** Four largemouth bass, collected by electro-shocking from Lake Chesdin in Chesterfield, VA, were held in a 0.05 hectare pond at the aquaculture pond complex of Virginia State University located on Randolph Farm in Chesterfield, VA. Bass were caught by hook and line using tadpoles as bait and placed in separate tanks for about four weeks and fed tadpoles two or three times a week to ensure that they would feed in experimental tanks. Since tadpoles were not used in feeding trials, this pretreatment should not bias bass in favor of any of the prey species.

A flow-through system consisting of six 1,135-liter (300-gallon) circular tanks was used to conduct experimental trials (four tanks) and to hold prey fish (two tanks). Water was pumped from an adjacent 0.05 hectare aquaculture pond to each tank and drained back into the source pond. Tanks were equipped with an external canister filter (Appendix II). Prey fish were fed daily with commercial aquaculture ration. A table-like structure, constructed with peg board and PVC piping, provided shelter in tanks for the bass (Appendix III). A large movable mirror ( $91.44 \text{ cm}^2$ ) was suspended over the tanks at an approximately  $65^\circ$  angle to enable observation at a distance with minimal disturbance of the bass (Appendix IV). This research was conducted as part of a broader research study (USDA/CREEES Evans-Allen program grant VAX-0209345 to Dr. Scott H. Newton, Agricultural Research Station, Virginia State University, Petersburg) that was approved by the Virginia State University Institutional Animal Care and Use Committee.

A total of 12 feeding trials with each bass were conducted two to three times a week over a five week period in July and August 2009. A fish of each prey species was measured for total length (TL) in centimeters and transferred simultaneously into a bass tank. Observations were made at a short distance from the tank using the mirror as an aide. Behaviors including strikes, releases, ingestion times, ingestion angles (head-first or tail-first for catfish), chase times and periods of bass inactivity were recorded using a handheld voice recorder either until all three fish were ingested or for 30 minutes. Remaining prey fish were removed from the tank.

**FEEDING TRIALS ANALYSIS:** Data from voice recordings were entered into JWatcher, a software packaged designed to quantify behavior by creating a detailed timeline of the events of each trial and by calculating statistics. With SPSS 17 Statistics software, chi-square tests were used to compare order of ingestion for each prey and to compare selectability index scores. This index was calculated to include difference in prey choice order by assigning a higher score for earlier ingestions. Numbers were multiplied by 3 for prey chosen first, by 2 for second, and by 1 for third. JWatcher was used to create a transitional probability matrix for order of prey consumption. It calculates the probability that a certain behavior will follow another behavior. This feature was used to calculate the probabilities of ingestion orders of the three prey species for each bass combined.

For each prey, mean chase time, mean ingestion time, mean number of strikes, and mean percent (arcsine transformed) of successful strikes were averaged for each bass as an n of 1 and compared with analysis of variance (ANOVA) blocked by bass and LSD post-hoc testing. In order to approximate normality, the data were log-transformed for ingestion time and chase time analyses. Initial failure of one bass to pursue and attack prey resulted in low chase times. This skewed results, therefore this bass was excluded from chase time analysis though it was included



in the graph. The mean head-first and tail-first catfish ingestion times were averaged for each bass and compared with a paired t-test. Because of the small sample sizes for these analyses, we accepted a significance level of  $\alpha = 0.10$  in two cases.

**JAR TRIALS:** After conclusion of the feeding trials, bass were exposed to all three prey species in separate covered gallon glass jars filled with water. The jars were held by scaffolding at the same height, thereby removing differences in prey positioning that could affect bass choice of prey species under tank conditions. Fish were randomly placed in the left, right, or center jar, and all three were simultaneously submerged in the tank for five minutes (Appendix I). The time spent by bass clearly oriented towards each species was recorded. For most trials, bass charged the jars and attempted to attack the prey inside, or remained within a few inches of a particular jar while bilaterally fixating on the target fish. As reinforcement, each bass was given the prey fish to which it displayed longest upon conclusion of each trial. Jar trials were conducted every two days for a total of five trials for each of the four bass.

**JAR ANALYSIS:** Data from each trial were entered into JWatcher, which calculated the total time of display towards each of the three prey species. Times were averaged for each bass, and means were compared with ANOVA blocked by bass followed by an LSD post-hoc test.

## RESULTS

**FEEDING TRIALS:** The three prey species had relatively similar size ranges. Goldfish ranged from 9 to 14 cm TL (mean  $\pm$  SD =  $12.31 \pm 1.27$  cm), bluegill from 8 to 13 cm ( $10.33 \pm 1.10$  cm), and channel catfish from 10 to 15 cm ( $11.96 \pm 1.12$  cm).

Half (49%) of all first ingestions were of goldfish, 29% catfish and 22% bluegill. Second ingestions were equal between goldfish and bluegill (40%), and lower (20%) for catfish. Third ingestions, when most goldfish were already removed, were bluegill (44%), catfish (39%) and goldfish (17%) (Table 1, Figure 1A). The order of ingestion is significant at  $\alpha = 0.1$  [ $p = 0.078$ ;  $\chi^2 = 8.408$ ; df = 4]. Selectability scores are different [ $p = 0.0086$ ;  $\chi^2 = 13.63$ ; df = 4], and goldfish had the highest total with 100 points (66 points for first ingestions, 30 for second ingestions, and 4 for third), followed by bluegill with 70 points (30 points each for first and second ingestions and 10 for third). Catfish had the lowest score with 64 points (39 points for first ingestions, 16 for second, and 9 for third) (Figure 1B).

The transitional probability matrix indicates that after a goldfish ingestion there is a 68% chance that bluegill and a 32% chance that catfish will be ingested next. After a bluegill ingestion there is a 53% chance that goldfish and a 47% chance that catfish will be ingested next. Finally, after a catfish ingestion there is a 59% chance that goldfish and a 41% chance that a bluegill will be ingested next (Figure 2).

Bass spent  $273.7 \pm 146.8$  s,  $142.3 \pm 80.8$  s, and  $14.5 \pm 4.2$  s chasing catfish, bluegill and goldfish, respectively (Figure 3A). Mean time chasing each prey per trial was significantly

different [ $F_{2,4} = 8.277$ ;  $p = 0.038$ ], specifically between goldfish and catfish [ $p = 0.016$ ]. The greater chase times for catfish and bluegill do not indicate a preference, but rather reflect the repeated release and recapture of these prey due to the increased handling caused by spines. Some chase times were near zero seconds, which would reflect an immediate successful strike. Longer chase times reflect the total time of several incidences of chases per trial. Many strikes were preceded by chases that occurred too quickly to record, particularly for goldfish. Mean ingestion times were  $147.7 \pm 68.7$  s,  $92.1 \pm 27.8$  s, and  $24.6 \pm 11.9$  s for catfish, bluegill and goldfish, respectively. The mean ingestion time for each prey was significantly different [ $F_{2,6} = 6.130$ ;  $p = 0.035$ ], specifically between goldfish and bluegill [ $p = 0.031$ ] and goldfish and catfish [ $p = 0.018$ ] (Figure 3B). For catfish ingestions, there was a significant difference in mean ingestion time between head-first and tail-first orientation [ $t_3 = 3.824$ ;  $p = 0.016$ ]. Bass took twice as long to ingest catfish tail-first [ $241.5 \pm 84.0$  s] than head-first [ $106.6 \pm 60.7$  s] (Figure 3C), likely because catfish locked spines when being ingested tail-first. Catfish ingestion times exhibited the greatest variation. In some cases catfish may be swallowed efficiently and in others complications from the spine prolong the process (Figure 4).

Most strikes were toward bluegill [ $41 \pm 40$ ], slightly fewer toward catfish [ $39 \pm 44$ ], and least for goldfish [ $13 \pm 8$ ], however differences were not significant [ $F_{2,6} = 4.740$ ;  $p = 0.149$ ] (Figure 5A). The high number of strikes on catfish and bluegill again reflect the difficulty in successful capture and ingestion. The mean percentage of successful strikes (strikes resulting in ingestion) was significant at  $\alpha = 0.1$  [ $F_{2,6} = 3.860$ ;  $p = 0.084$ ]. Most strikes were successful for goldfish [ $80.2 \pm 1.0\%$ ], less successful for bluegill [ $58.9 \pm 7.8\%$ ] and least successful for catfish [ $41.5 \pm 19.9\%$ ] (Figure 5B). Significant differences were between goldfish and bluegill [ $p = 0.060$ ] and bluegill and catfish [ $p = 0.047$ ].

**JAR TRIALS:** There was a significant difference in time (seconds) orienting toward the different species [ $F_{2,4} = 4.982$ ;  $p = 0.0392$ ]. Bass spent the most time oriented towards goldfish [ $54.5 \pm 16.1$  s], less for bluegill [ $48.6 \pm 15.4$  s], and the least for catfish [ $16.4 \pm 2.4$  s] (Figure 6). Significant differences occurred between goldfish and catfish [ $p < 0.05$ ].

**BEHAVIORAL OBSERVATIONS:** All bass exhibited frequent periods of inactivity throughout the trials. Catfish usually remained on the bottom of the tank along the perimeter, but during these inactive periods, they often swam directly alongside the length of the bass' body and often positioned themselves directly underneath the bass' tail. Bass often disgorged and re-attacked prey, specifically catfish and bluegill. Catfish seemed more able to survive after an attack, but bluegills often began to visibly weaken after being disgorged. Many times bass would not re-attack a bluegill that appeared injured from previous attacks. Bluegills were the least active of any of the three prey and were most often positioned towards the top of the water column along the perimeter of the tank. Goldfish did not favor any particular position in the tank and were the most active of the three prey. Goldfish were either gold or black, and bass readily ate both color morphs. This suggests that bass did not eat more goldfish only because of an attraction to the bright color.

Prey fish in tank 2 behaved differently in the first few trials than prey in other tanks. Whereas the other three bass were active in all trials, the bass in tank 2 was completely inactive in the first three trials and failed to attack prey fish. It gradually became more active after the third trial, eating one fish in the fourth and fifth trials, then eating all three prey during all but one remaining trials. During inactive trials, the bass remained motionless along a shaded edge of the tank while the prey fish actively swam around the entire tank, even near the bass. Once the

bass began to actively pursue prey after the third trial, the prey fish were considerably less active during remaining trials.

Bass exhibited a few consistent behaviors when ingesting prey. On several occasions, a bass would strike at a prey while holding a previously-caught fish in its mouth. This often resulted in loss of the first fish, which was usually recaptured immediately. After ingesting a goldfish, the bass were often inactive for short periods of up to 2 minutes ( $68.6 \pm 11.0$  s). After regurgitating goldfish scales when ingestion was complete, bass immediately commenced pursuit of another fish. When ingesting catfish tail-first, pectoral spines were often wedged against the side of the mouth (Figure 4). The bass would often shake its head vigorously from side to side in an attempt to dislodge the pectoral spines or to reorient the position of the catfish in its mouth, and often exhibited gill flaring during these attempts.

## DISCUSSION

In this study we examined bass predation on relatively similarly-sized bluegill, channel catfish, and goldfish. Previous work by Boshier et al. (2006) suggested that the pectoral spine of channel catfish protects them from being successfully ingested, however it did not address the question of whether the spines deter attack. Here we explored this question by comparing ingestion times, chase times, strike success, and order of ingestion of the three prey species by largemouth bass. Boshier et al. (2006) found that bass will consume channel catfish when it is the only prey present. However, when other species are present as a buffer, bass may recognize physical differences and choose prey that lack spines and are easier to ingest than channel catfish. The feeding preference of predators based on size and density of prey has been widely studied, however few studies have addressed how other physical characteristics of prey fish affect choice. Our study provides insight into the mechanisms of prey choice by a gape-limited predator presented with species of varying antipredator adaptations. The results are consistent with our hypothesis that goldfish are preferred first, followed by bluegill and finally catfish. This conclusion is supported by examples of the degree of ingestion complication of each species.

The three prey species were all of relatively similar sizes, with bluegill in the intermediate size range. The results of the following analyses suggest that bluegill is an intermediate prey choice between catfish and goldfish, though not always statistically different from each. Orders of ingestion are suggestive of a preference for goldfish, which were ingested

first half the time. Preference between bluegill and catfish was unclear, so the selectability index was used to magnify preference by assigning a higher value for earlier ingestions, which should grant a higher score for a more preferred prey species. The index supported goldfish as most preferred, followed by bluegill, then catfish. This order of preference was also supported by the transitional probability matrix and jar trials, which indicate that bass recognize different prey species.

Handling time includes time spent chasing, capturing, and ingesting each prey (Holling 1959). Handling time is expected to be greater for larger or more difficult or dangerous prey (Forbes 1989). Results indicate that handling time is in fact greater for catfish, less for bluegill, and the least for goldfish. Chase time suggested bluegills were intermediate prey, but differences were only significant between goldfish and catfish. Shorter chase times for goldfish suggest it is the easiest prey to capture and ingest due to its soft-rayed and somewhat cylindrical body, where bluegill and catfish were often disgorged and chased again.

Tail-first ingestion time of catfish required twice as much time as head-first ingestion, which is consistent with results found by Emmett and Cochran (in press) in which largemouth bass took longer to ingest tadpole madtoms (*Noturus gyrinus*) tail-first when spines were abducted and locked. There was no indication that bass learned to capture catfish head-first over time. However, the repeated disgorging of catfish resulted in high numbers of unsuccessful strikes, and indicates that bass are sensitized to the spine and may attempt to recapture a catfish head-first if originally caught tail-first. This behavior is similar to observations made by Boshier et al. (2006), in which bass disgorged and recaptured catfish with spines more than clipped fish, resulting in a higher number of strikes for intact catfish. We also observed that bass frequently attempted to reorient catfish from a tail-first to a head-first position inside its mouth. The shaking

of prey and gill flaring observed while bass attempted to ingest catfish are also signs of discomfort (Emmett and Cochran, in press), and often resulted in disgorging of the catfish followed by reattempting strikes from a different angle.

During several trials catfish often swam along the length of the body, either next to or underneath the predator. This behavior is similar to “inspection behavior” (Kelley and Magurran 2006) in which prey fish often swim the length of a predator’s body as a way of signaling to the predator that its presence has been detected. This behavior may also allow the prey to determine the level of threat of the predator based on its apparent motivation to attack certain prey, often indicated by chemical cues (Brown 2003). Potential prey may behave differently following inspection based on the predator’s posture, excretion of chemical alarm cues, or other indications of the predator’s attack motivation (Brown 2003). This may explain the behavior of prey in tank 2 during periods of bass inactivity where predation risk may have been perceived as low, and therefore promoting increased activity of the prey. Predators are more likely to attack prey that has not inspected (Kelley and Magurran 2006), which may offer another explanation to bass choice against catfish as well as the avoidance of spines. In addition, catfish favored positioning themselves underneath the bass’ tail, which would make it difficult for the bass to turn around and capture the catfish before it could escape.

Prey fish must balance foraging behavior with predator avoidance, and a malnourished individual may accept greater risks of predation in order to feed than a well-fed individual (Brown 2003). A more vulnerable prey will exhibit less foraging activity and different habitat usage in the presence of a predator (Lima and Dill 1990; Chick and McIvor 1997; Creel et al. 2008), which consequently may effect growth and fitness. Prey activity level in these trials should not reflect nourishment levels, as all prey were fed to satiation daily. Goldfish, purchased



from a local commercial dealer, were the most active species. These fish likely had not been previously exposed to predators. Bluegills were least active, which is a common behavioral anti-predatory adaption in this species (Moody et al. 1983).

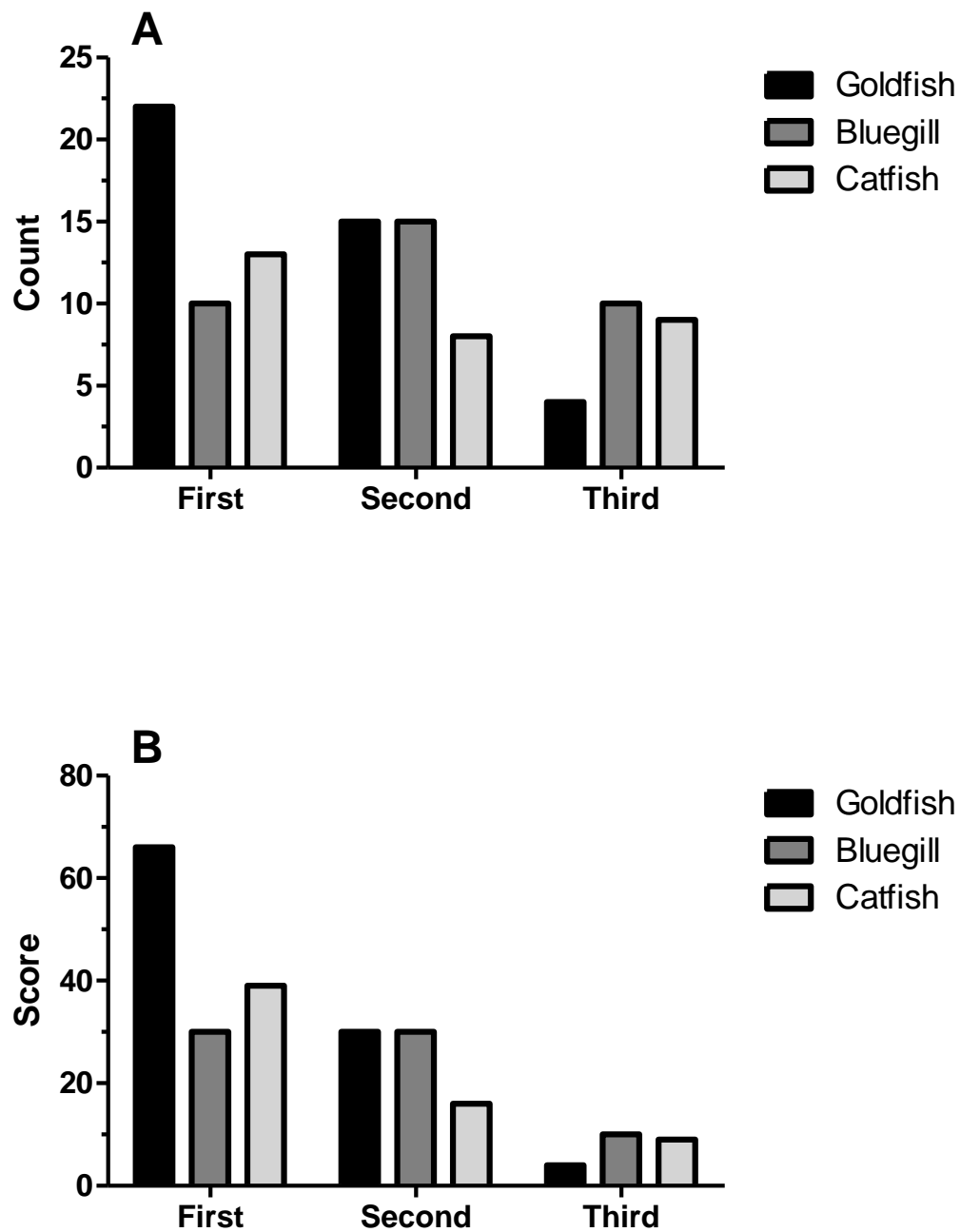
Similar balances also occur morphologically and, over time, malnourished prey may develop a body morphology that increases foraging ability, while well-fed prey may develop morphologies that are effective in deterring predation (Borcherding and Magnhagen 2007). Changes in morphology over time of various prey, such as perch (Kekäläinen et al. 2010) and carp (Brönmark and Miner 1992), were observed when exposed to constant predation. The effect of predator presence on spine morphology has not been studied although spines of aquaculture individuals are smaller and lighter than wild individuals of the same size, suggesting a relaxation of selection pressure in aquaculture fish (Duvall 2007).

In conclusion, bass appear to recognize different prey species. Part of this recognition may be that channel catfish are dangerous prey and difficult to ingest, and bass will tend to avoid them if alternative prey are available. Bluegill and goldfish are already important foraging stock for largemouth bass in aquaculture. If stocked with channel catfish, these buffer species may greatly increase survival of channel catfish juveniles until they grow to less vulnerable sizes. Our results therefore have implications for stocking success in aquaculture and recreationally fished locations. Bass from Lake Chesdin are exposed to channel catfish, sunfish and various cyprinids but would not typically encounter goldfish. Interactions similar to those observed in our study may occur in the wild between species of similar body morphologies to prey used in this study. If this is the case, bass may regularly feed on minnows (family Cyprinidae), juvenile carp, or other prey with similar body types to goldfish, and may show a preference for these types over channel catfish or bluegill.

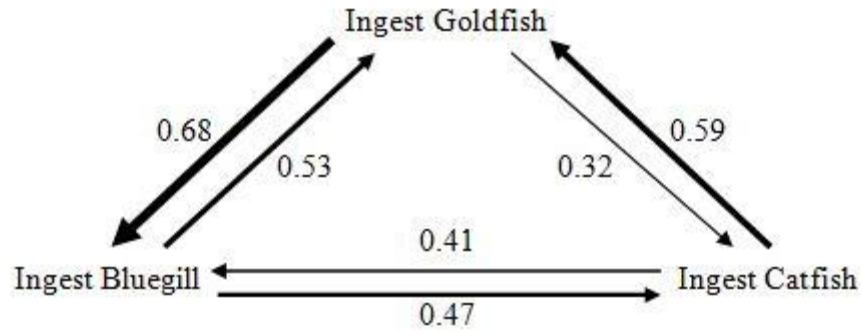
## TABLES AND FIGURES

**TABLE 1. CONTINGENCY TABLE FOR ORDER OF INGESTION**

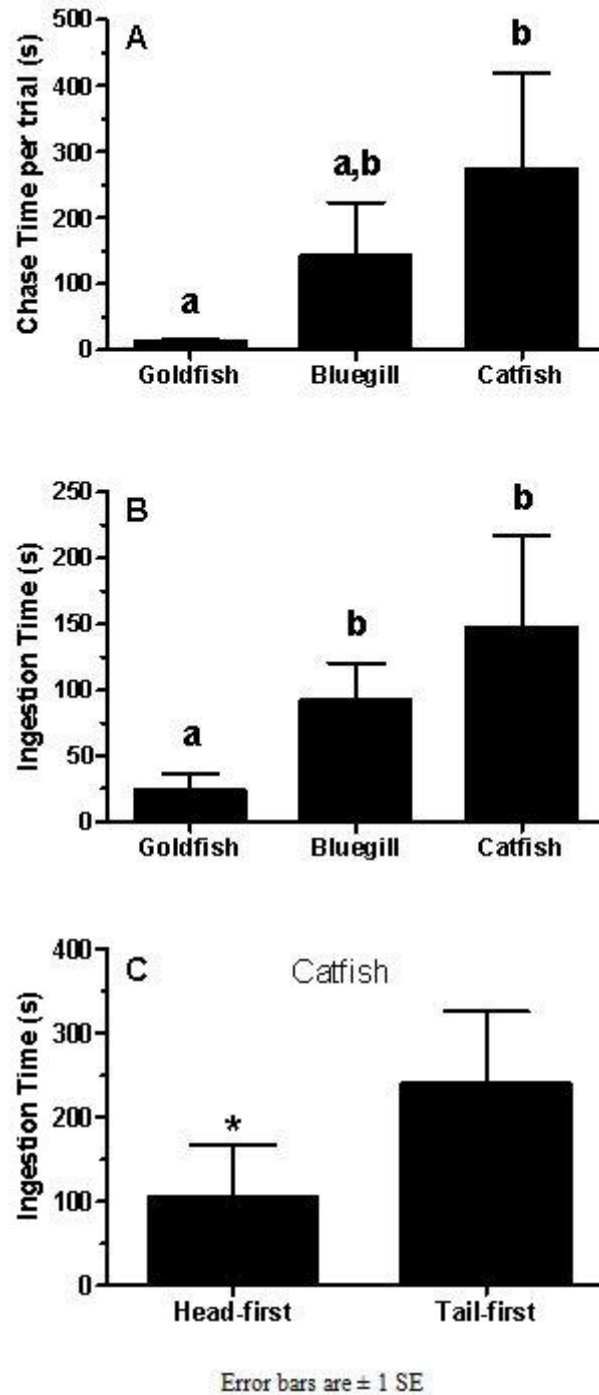
			Prey			Total
			Goldfish	Bluegill	Catfish	
Order of Ingestion	First	Count	22	10	13	45
		Expected Count	17.4	14.9	12.7	45.0
		% within Order of Ingestion	48.9%	22.2%	28.9%	100.0%
		% within Prey	53.7%	28.6%	43.3%	42.5%
		% of Total	20.8%	9.4%	12.3%	42.5%
	Second	Count	15	15	8	38
		Expected Count	14.7	12.5	10.8	38.0
		% within Order of Ingestion	39.5%	39.5%	21.1%	100.0%
		% within Prey	36.6%	42.9%	26.7%	35.8%
		% of Total	14.2%	14.2%	7.5%	35.8%
	Third	Count	4	10	9	23
		Expected Count	8.9	7.6	6.5	23.0
		% within Order of Ingestion	17.4%	43.5%	39.1%	100.0%
		% within Prey	9.8%	28.6%	30.0%	21.7%
		% of Total	3.8%	9.4%	8.5%	21.7%
Total	Count		41	35	30	106
	Expected Count		41.0	35.0	30.0	106.0
	% within Order of Ingestion		38.7%	33.0%	28.3%	100.0%
	% within Prey		100.0%	100.0%	100.0%	100.0%
	% of Total		38.7%	33.0%	28.3%	100.0%



**Figure 1.** (A) Number of first, second, and third ingestions by largemouth bass for goldfish, bluegill, and channel catfish. (B) Scores of each prey as calculated by the selectability index.



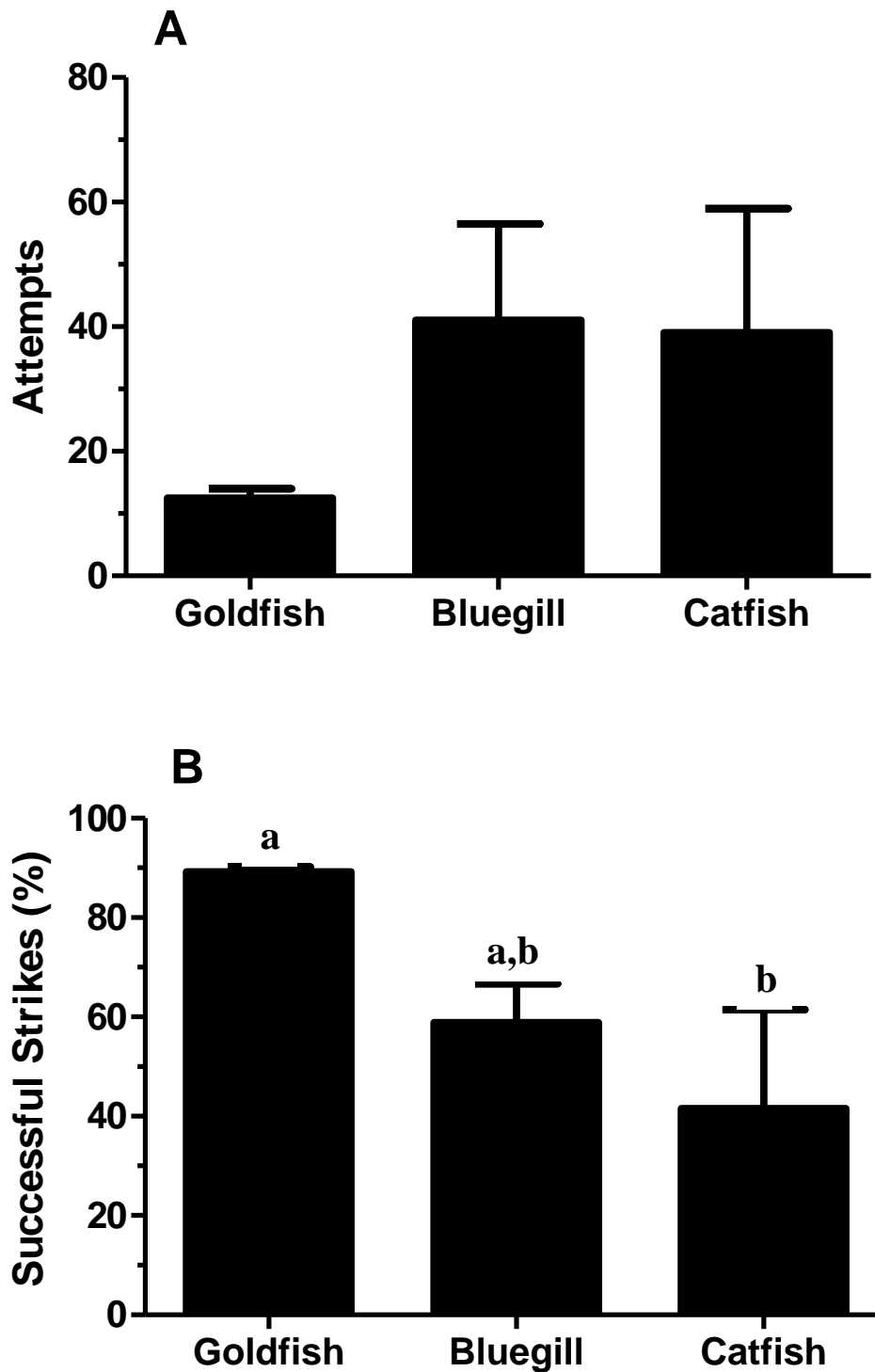
**Figure 2.** Transitional probability diagram for order of ingestion; the probabilities indicate the likelihood that the specified prey will be ingested following ingestion of the prey at the arrow's origin. Thicker arrows indicate higher probabilities of ingestion. For example, if a bass ingests a goldfish first, there is a 68% chance that bluegill will be ingested next, and a 32% chance that catfish will be ingested next.



**Figure 3.** (A) Mean time per trial that largemouth bass spent chasing goldfish, bluegill, and channel catfish. (B) Mean ingestion time per prey, and (C) mean ingestion time for head-first versus tail-first ingestion of channel catfish.

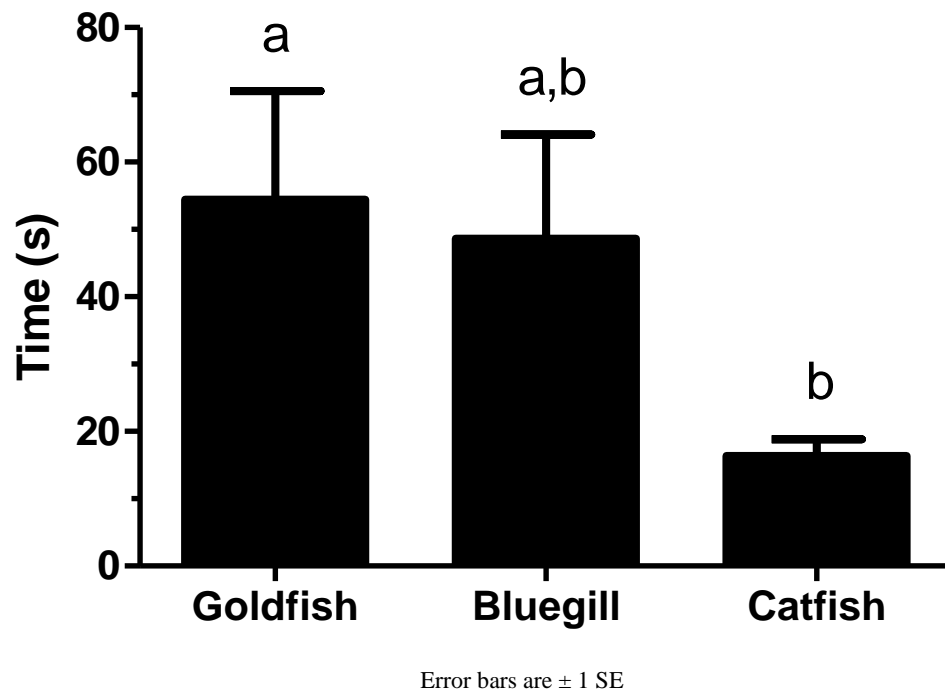


**Figure 4.** Photo showing largemouth bass with channel catfish in its mouth. The catfish is upside down, and its right pectoral spine is hooked in the corner of the bass' mouth (indicated by arrow), making it impossible for the bass to swallow without repositioning the catfish.



Error bars are  $\pm 1$  SE

**Figure 5.** (A) Mean number of attempted strikes by largemouth bass of goldfish, bluegill, and channel catfish. (B) Mean percent of successful strikes per prey.



**Figure 6.** Mean orientation time of largemouth bass toward jars with goldfish, bluegill, and channel catfish.



## *Chapter II. An Experimental Study of Bass Feeding Preference*

### **INTRODUCTION**

Predators exert direct and indirect effects on prey populations. Indirect effects influence habitat selection, competition, and growth through density- and size-dependent mechanisms and may be of greater importance than direct effects, i.e. consumption (Abrams 1984). When a fish detects a predator it exhibits behaviors to reduce predation risk (Wisenden and Harter 2001). Predators may cause smaller or more vulnerable prey to seek safer areas (Mittelbach 1986), thus segregating prey within habitats. If safe habitats are resource-poor, then habitat segregation could affect growth rates and inter- and intra-specific competition. For example, for fish species such as bluegill (*Lepomis macrochirus*) with similar resource requirements between juveniles and adults, habitat segregation of small individuals may cause stunted growth (Werner et al. 1983; Mittelbach 1986). Predators may also affect a third trophic level, i.e. the food sources of the prey fish. For instance, clustering of fish in less hazardous areas may also affect populations of benthic invertebrates. Gilliam et al. (1989) found large population reductions and increased evenness in the benthic invertebrate communities in refuge areas.

Channel catfish (*Ictalurus punctatus*) are often stocked in ponds and lakes for aquaculture (Dudash and Heiginger 1996) and recreational fishing (Bonar et al. 1997). In water bodies with established populations of largemouth bass (*Micropterus salmoides*), survival of newly-stocked channel catfish is low (Spinelli et al. 1985). Bass predation can reduce populations and impact

the growth and fitness of individuals (Krummrich and Heidinger 1973; Dudash and Heidinger 1996; Katano et al. 2005; Kekäläinen et al. 2010). Largemouth bass are gape-limited predators and cannot ingest prey above a certain size (Katano et al. 2005). Channel catfish possess pectoral and dorsal spines that allow them to increase their effective size and complicate ingestion by gape-limited predators. The pectoral spine can be bound and locked utilizing derived processes at the base of the spine that mate with counterparts in the girdle (Fine et al. 1997). These capabilities render catfish dangerous to ingest and may result in injury to predators such as fish (Krummrich & Heidiger 1973; Pimental et al. 1985; Ryden & Smith 2002), snakes (Burr & Stoeckel 1999) and birds (Bunkley-Williams et al. 1994; Werner et al. 2001).

Forbes' dangerous prey hypothesis states that prey should avoid dangerous species in favor of safer ones (Forbes 1989). Predators, including largemouth bass, may learn to visually recognize and avoid dangerous prey (Hoogland et al. 1956; Britson 1998; Glahn and Dorr 2000; Boshier et al. 2006; Holt and Johnston 2009). Once exposed to the pectoral spines, bass may recognize and avoid channel catfish as well. Boshier et al. (2006) found that bass will consume channel catfish when it is the only prey present. With the addition of buffer prey species, bass may differentiate between dangerous prey with spines and safer prey, and therefore choose the alternative prey.

For this study, we presented largemouth bass with catfish and two alternative prey species, namely bluegill sunfish and goldfish (*Carassius auratus*) in net-pens. The deep-bodied, compressed morphology of the sunfish, along with the spiny dorsal fin (Jenkins and Burkhead 1993), is considered a mechanism for predator deterrence as seen in other deep-bodied species such as perch (Kekäläinen et al. 2010). The goldfish is soft-rayed and has an intermediate body type between deep-bodied fish and other more cylindrical minnows (family Cyprinidae).

Goldfish are close relatives of carp, and Brönmark and Miner (1992) found that in lakes stocked with pike as a predator, crucian carp (*Carassius carassius*) developed deeper bodies compared to unexposed conspecifics. Moody et al. (1983) found that tiger muskellunge (*Esox masquinongy* x *E. lucius*) preferred fathead minnows (*Pimephales promelas*) over bluegills and concluded that bluegill were less susceptible to predation because of the deeper body and spiny-rayed dorsal fin. Wahl and Stein (1988) noted differences between capture success of bluegills and gizzard shad (*Dorosoma cepedianum*), which has a similar deep-body to bluegill but no spines, suggesting that body-depth and spines both function in prey preference of esocids, namely tiger muskellunge, muskellunge (*E. masquinongy*), and northern pike (*E. lucius*). We hypothesize that morphological characteristics of prey may influence feeding preferences of other piscivores such as the largemouth bass, and that goldfish will be preferred over bluegill and bluegill over catfish. We exposed bass to populations of different combinations of the three similarly-sized prey types and compared numbers ingested. The results provide insight into the prey preference of bass and whether catfish consumption changes in the presence of alternative prey types.

## METHODS

Three mesh net pens (3 x 5 x 2 m) were submerged into each of three ¼-acre ponds at the Virginia State University Aquaculture Center pond complex located on Randolph Farm in Chesterfield County, Virginia. In three separate trials, sixty prey fish in different species combinations were measured for total length (TL) and placed in each pen with a largemouth bass, which were collected by electro-shocking from Lake Chesdin, Chesterfield, VA. Prior to initiating the study, bass were maintained in an ⅛-acre pond and fed tadpoles to reduced bias toward any of the prey species used in the trials. Bass were caught by hook and line using tadpoles as bait, and one bass was stocked into each of the nine net pens. Bass ranged from 35.1 to 48.4 cm TL (mean  $\pm$  SD = 40.7  $\pm$  4.3 cm). Pens were harvested after 15 days for the first trial and 10 days for the second and third trials. Number eaten was determined by subtraction (dead fish were removed daily). Sizes of survivors were compared with those of consumed individuals with independent t-tests with a significance at  $\alpha = 0.05$ . Maximum and average TL (cm) as well as total weight consumed (g) of each prey eaten were plotted against bass TL (cm). Since only TL of fish was measured during trials, the weight of each fish was estimated by regression equations created using length/weight data obtained from various sources for each prey (Appendices I-III). Methods were approved by the Virginia State University Institutional Animal Care and Use Committee.

TRIAL ONE: The first trial was conducted using bluegill sunfish and channel catfish to determine prey-size preferences of the bass, and the number consumed in non-choice and choice

trials. We stocked two replicates of each of the following combinations of prey: 60 catfish, 60 bluegills, and 30 catfish and 30 bluegills. In each case half of the fish were in the smaller half of the size range and half in the large. Small catfish ranged from 13 to 18 cm TL (mean  $\pm$  SD =  $16.8 \pm 1.2$  cm) and large ones from 19 to 24 cm ( $20.7 \pm 1.5$  cm), small bluegill from 8 to 12 cm ( $9.5 \pm 1.1$  cm), and large ones from 12 to 15 cm ( $12.9 \pm 1.0$  cm). Pens were stocked on May 26<sup>th</sup> and harvested on June 10<sup>th</sup>, 2009. The number of each prey eaten was compared within pen types (choice and non-choice) with a one-tailed binomial test, which determines a difference from a 50/50 ratio. Manly's  $\alpha$  was used to quantify preference of prey types when a prey population decreases over time (Krebs 1989). Since prey fish were not replaced after consumption, the index was calculated for each prey species using:

$$\alpha_i = \log p_i / \sum \log p_i,$$

where  $p_i$  is the proportion of prey alive at the end of the trial, calculated for each of the prey species. Manly's  $\alpha$  was compared with a paired t-test between prey types in choice pens.

TRIAL TWO: Pens were stocked with various combinations of goldfish, bluegills and catfish. Prey sizes were kept as close as possible, depending on availability. We stocked three replicates (one per pond) of the following combinations: 30 bluegill and 30 channel catfish, 30 goldfish and 30 channel catfish, and 30 bluegill and 30 goldfish. Pens were stocked on July 14<sup>th</sup> and harvested on July 24<sup>th</sup>, 2009. Goldfish ranged from 8.6 to 15.7 cm TL ( $12.3 \pm 1.2$  cm), bluegill from 7.4 to 15.3 cm ( $10.6 \pm 1.7$ cm), and catfish from 11.4 to 19.5 cm ( $16.2 \pm 2.0$  cm). Number of prey eaten was compared with binomial tests and Manly's  $\alpha$  values for each prey were compared with paired t-tests for each prey pairing.

TRIAL THREE: The nine pens were stocked with one bass and 20 of each prey species. Goldfish ranged from 9.3 to 18.9 cm TL ( $13.1 \pm 1.4$  cm), bluegill from 7.7 to 15.7 cm ( $11.0 \pm 1.3$

cm), and catfish from 11.3 to 19.7 cm total length ( $16.1 \pm 2.0$  cm). Pens were stocked on August 4<sup>th</sup> and harvested on August 14<sup>th</sup>, 2009. ANOVA blocked by bass was used to compare numbers of each prey eaten and Manly's  $\alpha$  preferences for each prey across the nine pens with an LSD post-hoc test.

## RESULTS

TRIAL ONE: Bass ate 31 catfish and 44 bluegill in non-choice trials [ $p = 0.082$ ], and 16 catfish and 43 bluegill in choice trials [ $p = 0.0001$ ] (Figure 7). Manly's  $\alpha$  was greater for bluegill [ $0.78 \pm 0.13$ ] than for catfish [ $0.22 \pm 0.13$ ] but was not significantly different [ $p = 0.274$ ] (Figure 8). In pens stocked with 30 catfish and 30 bluegill, bass were more likely to eat smaller [ $17.5 \pm 0.5$  cm] than larger catfish [ $19.5 \pm 0.3$  cm;  $t_{58} = 3.009$ ;  $p = 0.004$ ] and smaller [ $10.2 \pm 0.3$  cm] than larger bluegill [ $12.7 \pm 0.3$  cm;  $t_{58} = 5.742$ ;  $p = 0.000$ ] (Figures 9a and b). For pens stocked only with catfish, bass ate smaller catfish [ $16.8 \pm 0.4$  cm to  $19.2 \pm 0.2$  cm;  $t_{118} = 5.320$ ;  $p = 0.000$ ] (Figure 9c), and for pens stocked with 60 bluegill, bass ate smaller bluegill [ $9.4 \pm 0.2$  cm to  $12.5 \pm 0.2$  cm;  $t_{118} = 12.734$ ;  $p = 0.000$ ] (Figure 9d). Generally larger bass ate larger prey, but there was no significant relationship between average or maximum prey TL or weight and bass TL (Figure 10).

TRIAL TWO: Bass ate similar numbers of goldfish and bluegills [ $17 \pm 5$  and  $16 \pm 4$  respectively;  $p = 1.000$ ] (Figure 11a). However, fewer catfish were consumed than either goldfish [ $16 \pm 5$  to  $5 \pm 3$ ;  $p = 0.000$ ] or bluegill [ $16 \pm 2$  to  $3 \pm 0$ ;  $p = 0.000$ ] (Figures 11b and c). Manly's  $\alpha$  was not different between goldfish and bluegill pairings [ $0.51 \pm 0.04$  and  $0.49 \pm 0.04$ , respectively;  $t_2 = 0.326$ ;  $p = 0.776$ ] (Figure 12) but was less for catfish [ $0.11 \pm 0.04$ ] than goldfish [ $0.89 \pm 0.04$ ;  $t_2 = 8.622$ ;  $p = 0.013$ ] and catfish [ $0.12 \pm 0.01$ ] than bluegill [ $0.88 \pm 0.01$ ;  $t_2 = 32.909$ ;  $p = 0.001$ ]. Bass ate smaller bluegill [ $10.1 \pm 0.1$  cm to  $11.5 \pm 0.2$  cm;  $t_{151} = 5.683$ ;  $p = 0.000$ ], smaller goldfish [ $12.1 \pm 0.1$  cm to  $13.0 \pm 0.1$  cm;  $t_{178} = 5.238$ ;  $p = 0.000$ ], and smaller

catfish [ $15.0 \pm 0.4$  cm to  $16.8 \pm 0.2$  cm;  $t_{176} = 4.029$ ;  $p = 0.000$ ] (Figure 13). Again, larger bass ate larger prey, but there was no significant correlation of prey and bass size (Figure 14).

TRIAL THREE: There were significant differences among prey eaten [ $F_2 = 6.527$ ;  $p = 0.023$ ], and bass ate similar numbers of goldfish [ $5 \pm 1$ ] and bluegill [ $7 \pm 2$ ;  $t_8 = 1.159$ ;  $p = 0.093$ ], more goldfish than catfish [ $1 \pm 0$ ;  $t_8 = 4.124$ ;  $p = 0.001$ ] and more bluegill than catfish [ $t_8 = 3.457$ ;  $p = 0.003$ ] (Figure 15). Manly's  $\alpha$  values for each prey were significantly different [ $F_2 = 8.045$ ;  $p = 0.003$ ]. Preferences for goldfish [ $0.37 \pm 0.21$ ] and bluegill [ $0.49 \pm 0.25$ ] were similar [ $t_9 = 0.870$ ;  $p = 0.136$ ], but both bluegill [ $t_9 = 4.164$ ;  $p = 0.000$ ] and goldfish [ $t_9 = 4.734$ ;  $p = 0.000$ ] were preferred to catfish [ $0.09 \pm 0.07$ ] (Figure 16). Bass ate smaller goldfish [ $13.3 \pm 0.2$  cm to  $13.7 \pm 0.1$  cm;  $t_{178} = 5.357$ ;  $p = 0.000$ ], smaller bluegill [ $10.7 \pm 0.2$  cm to  $11.4 \pm 0.1$  cm;  $t_{176} = 3.713$ ;  $p = 0.000$ ], and smaller catfish [ $13.4 \pm 0.3$  cm to  $16.7 \pm 0.2$  cm;  $t_{180} = 5.963$ ;  $p = 0.000$ ] (Figure 17). Larger bass tended to eat shorter catfish, but correlations between prey and bass size were still not significant (Figure 18).



## DISCUSSION

Predator avoidance mechanisms include deterrence and defense against predation, reducing probabilities of attack and increasing survivability of attacks, respectively (Bosher et al. 2006). Bosher et al. (2006) found that the pectoral spine of channel catfish decreases attack mortality: intact catfish were three times more likely to survive an hour session with a largemouth bass than comparably-sized individuals with spines clipped. Our study examined whether bass will avoid catfish and consume fewer catfish than alternative prey without pectoral spines. We conducted experiments at three different times, using combinations of two prey in some trials and all three in others.

Piscivore prey choice is associated with the density and size of prey species (Abrams 1984). When these factors are kept constant, predators will likely choose prey species based on behavioral or morphological features. Many prey species have adapted to predation pressures with changes in behavior or body morphology (Moody et al, 1983; Brönmark and Miner 1992; Kelley and Magurran 2006), suggesting that predators may choose alternative prey without these adaptations. Over time, natural selection may favor prey species with anti-predator behaviors or morphologies, possibly decreasing vulnerability to predation.

In the first trial, bass ate both bluegill and catfish when each was the only prey present. In combination pens bass ate significantly more bluegill than catfish. However, the numbers of catfish eaten declined only slightly from non-choice to choice pens. This may suggest that catfish are not avoided completely, and that catfish predation may be opportunistic while bluegill

predation is preferential. Many available catfish were not eaten, especially in the presence of bluegill, supporting the premise for the spine as an anti-predator adaptation. Second and third trials included goldfish, a third prey species that lacked bony spines and was somewhat more shallow-bodied than bluegill. There was no difference in numbers eaten between bluegill and goldfish, but fewer catfish were eaten than either of the other two species. This suggests that though goldfish are soft-rayed, the somewhat deep body causes no preference over bluegill. It is apparent that both alternative species are preferred over catfish, supporting the spines as a deterrent to predators. Results are further supported by Manly's  $\alpha$  preference values, which again indicate no difference between goldfish and bluegill and a preference for both species over catfish. We observed similar results in observational feeding studies in which numbers eaten, ingestion times, successful strikes, and chasing times were not different between goldfish and bluegill but differed from catfish. In trials in which bass were exposed simultaneously to the three species in jars, they showed a clear preference for goldfish (Nellis et al., unpublished).

The sizes of prey eaten in all trials indicate that bass of 35 to 48 cm TL prefer prey between 10 and 20 cm TL and suggest that the smaller prey will be consumed preferentially over larger individuals. There was no significant relationship between prey size and bass size for any of the trials, however generally larger bass ate larger prey with the exception of trial 3, during which larger bass seemed to prefer smaller catfish.

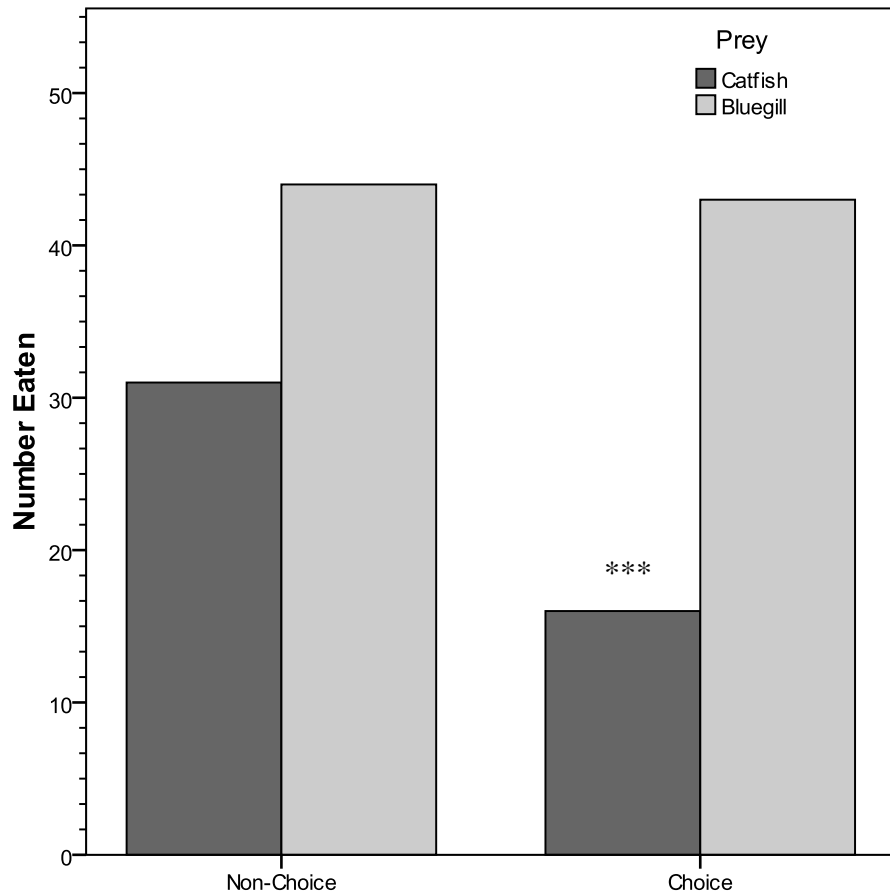
Reduced foraging behavior (Moody et al. 1983; Lima and Dill 1990; Chick and McIvor 1997; Creel et al. 2008) and schooling behavior (Kelley and Magurran 2006) are common anti-predator behaviors of fishes. Schooling behavior was noted in goldfish in the net pens, which were often seen swimming near the surface. Although schooling is considered an anti-predator adaptation, bass consumed more goldfish than catfish. Increased movement of goldfish within

the confines of the net pen may have made them more attractive targets, but may also strengthen the argument of avoidance of catfish. The gold color may have attracted bass attention as well, however our experience with feeding bass with both gold and black goldfish shows that bass will readily eat both (Nellis et al., unpublished). Reduced foraging activity in catfish in the presence of predators could not be observed in the net pens, but it has been demonstrated in tank experiments (Fine et al. submitted). Position of each species in the water column further supports bass avoidance of catfish. Catfish and bass remain near the bottom of the net pens and therefore bass would have had the greatest time exposure in close proximity to catfish. In other experiments, catfish inspected bass and positioned themselves directly underneath the tail (Nellis et al., unpublished). If this behavior occurred in the net pens, bass would have been closer to channel catfish in these cases as well. Bluegills typically swam near the surface and along the edges of the pens, and goldfish schooled in the middle to upper portion of the water column. Therefore bass had to expend more effort to attack the two alternative species. Similar consumption of goldfish and bluegills suggests that the somewhat deep body of goldfish complicates their consumption even with soft dorsal and anal fins. Our experience with golden shiners (*Notemigonus crysoleucas*), which have a cylindrical shape, indicates that bass would have rapidly consumed them. Deep body morphology seems to be an important adaptation in bluegills, relatives of goldfish, and other fish (Moody et al. 1983; Brönmark and Miner 1992; Kekäläinen et al. 2010). Prey consumption by bass decreased in the third trial, which occurred during the warmest part of the year, suggesting decreased metabolic activity of the bass (Johnston and Dunn 1987).

The well-developed spines of channel catfish (Fine et al. 1997) complicate consumption by bass (Bosher et al. 2006), and this study indicates that fewer catfish will be eaten if other prey

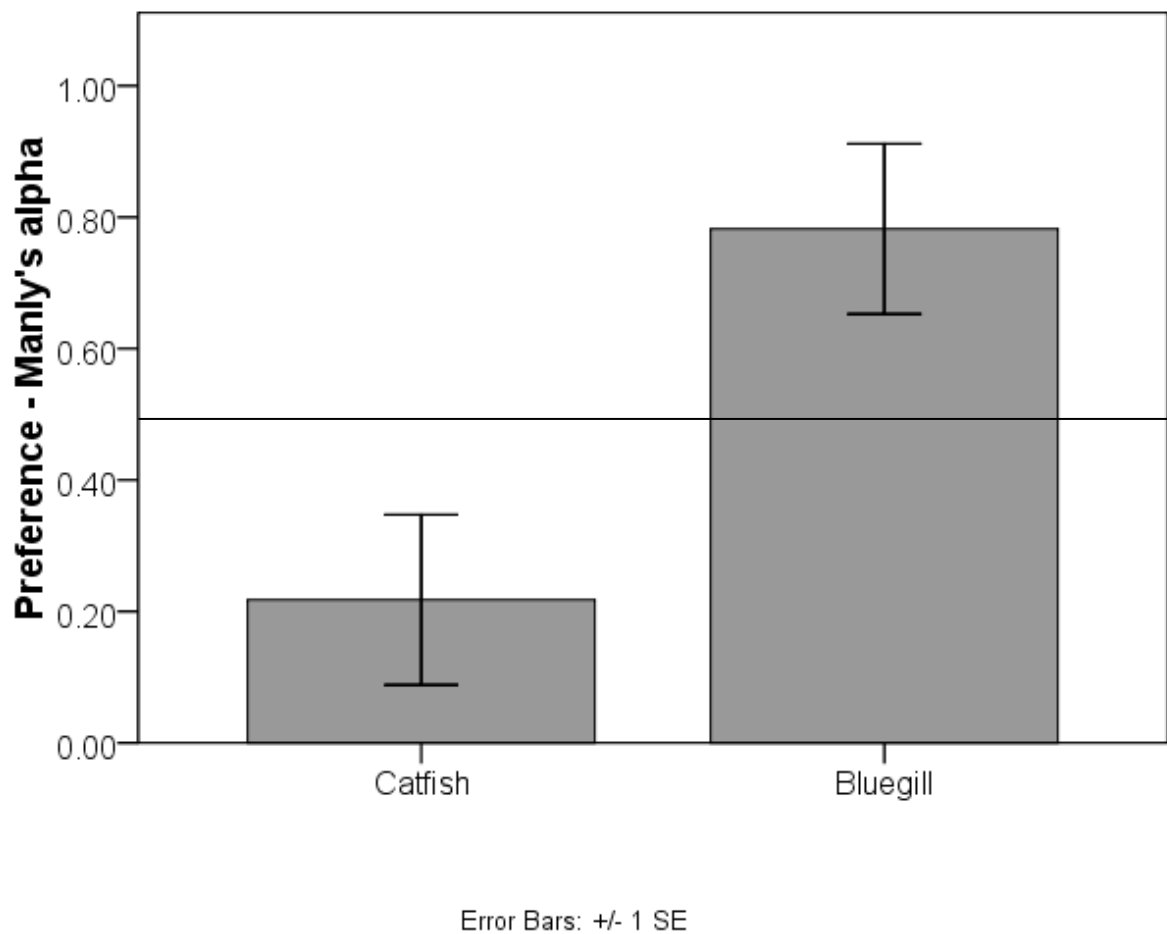
are available. Thus catfish spines appear to decrease predation in natural habitats and in stocked lakes and ponds with alternative prey. In aquaculture and in ponds or lakes stocked with channel catfish for recreational use, survival may be increased with the addition of alternative prey. Based on our results, prey fish of similar morphologies to bluegill and goldfish may both be effective alternatives. In natural habitats of bass and channel catfish, bluegills are a likely alternative.

## TABLES AND FIGURES

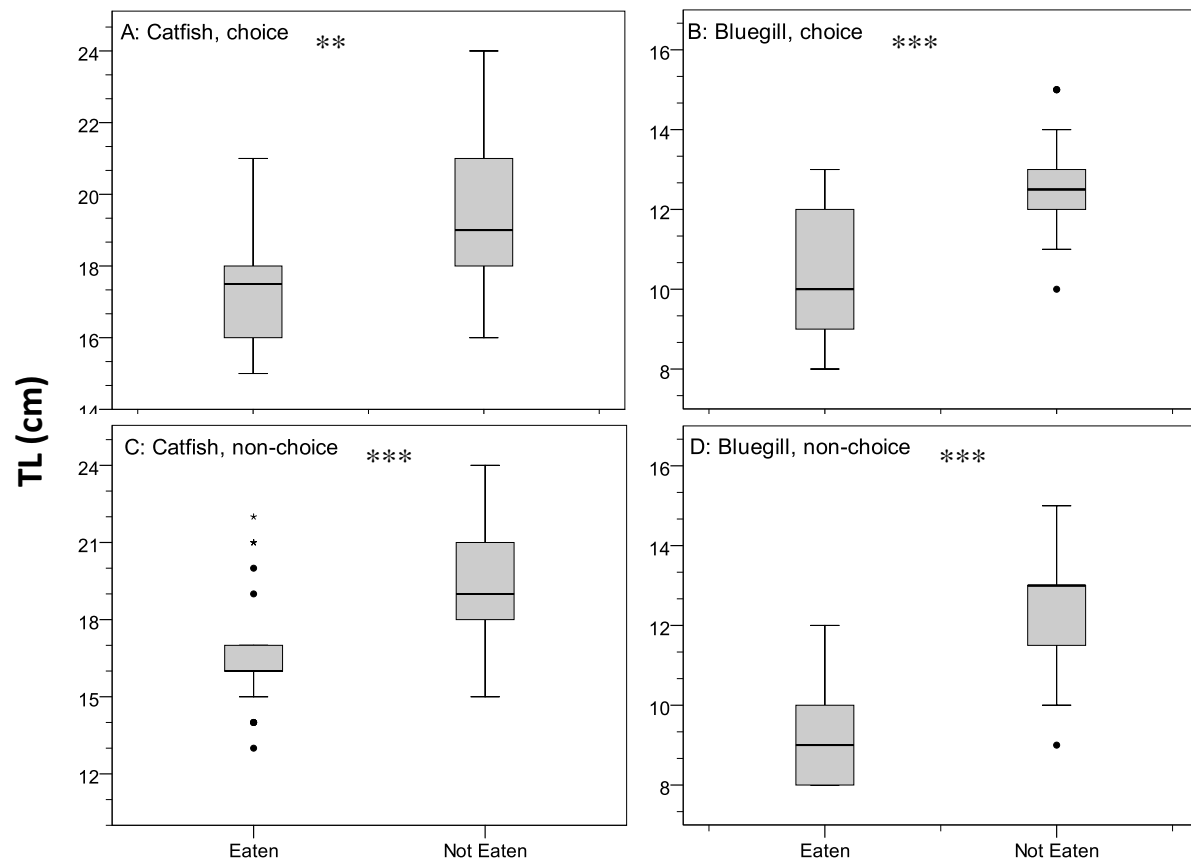


\*\*\* =  $p \leq 0.001$

**Figure 7.** Numbers of bluegill and channel catfish eaten by largemouth bass during the first net pen trial in choice and non-choice conditions.

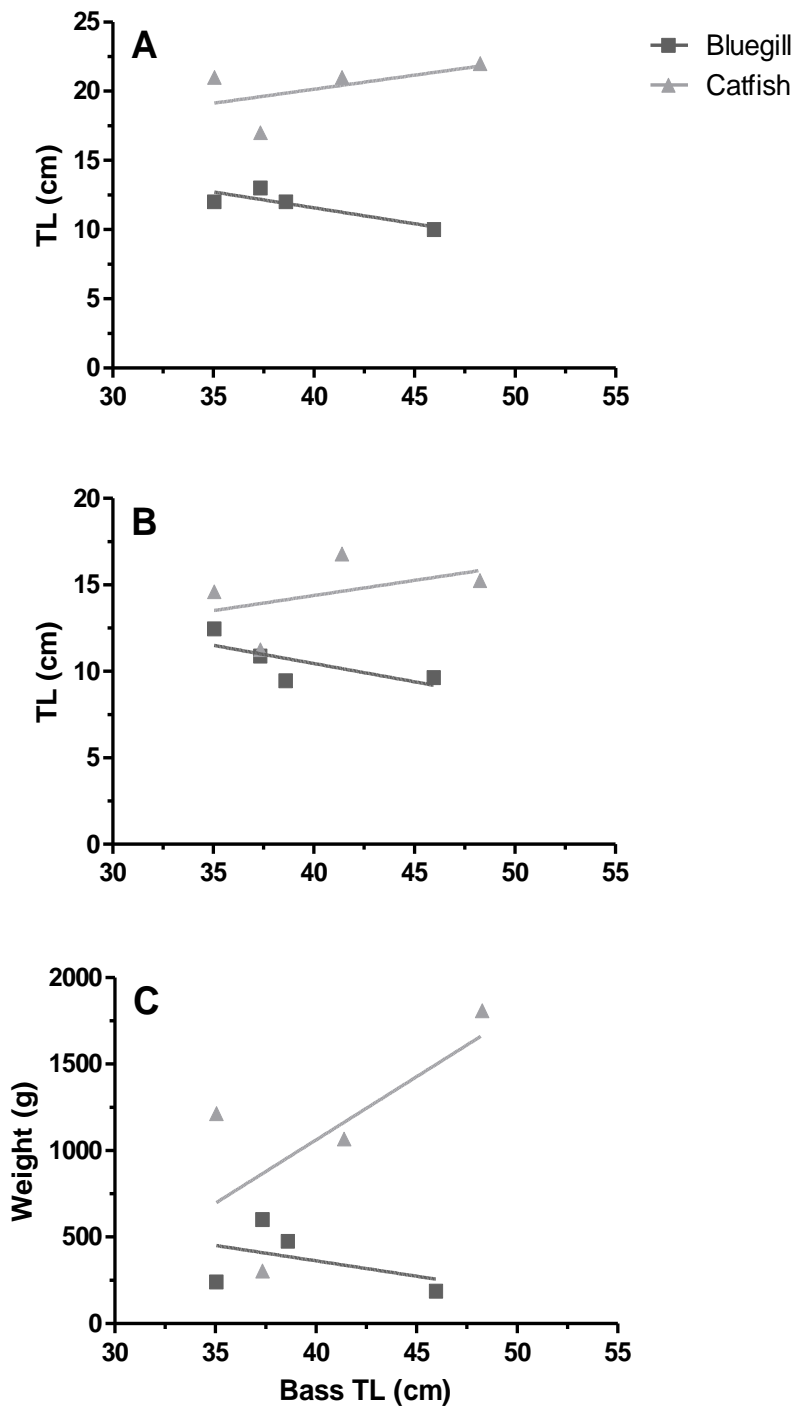


**Figure 8.** Manly's  $\alpha$  values calculated for the first net pen trial during which largemouth bass were presented with combinations of bluegill and channel catfish. The reference line indicates the expected preference of 50% for each prey.



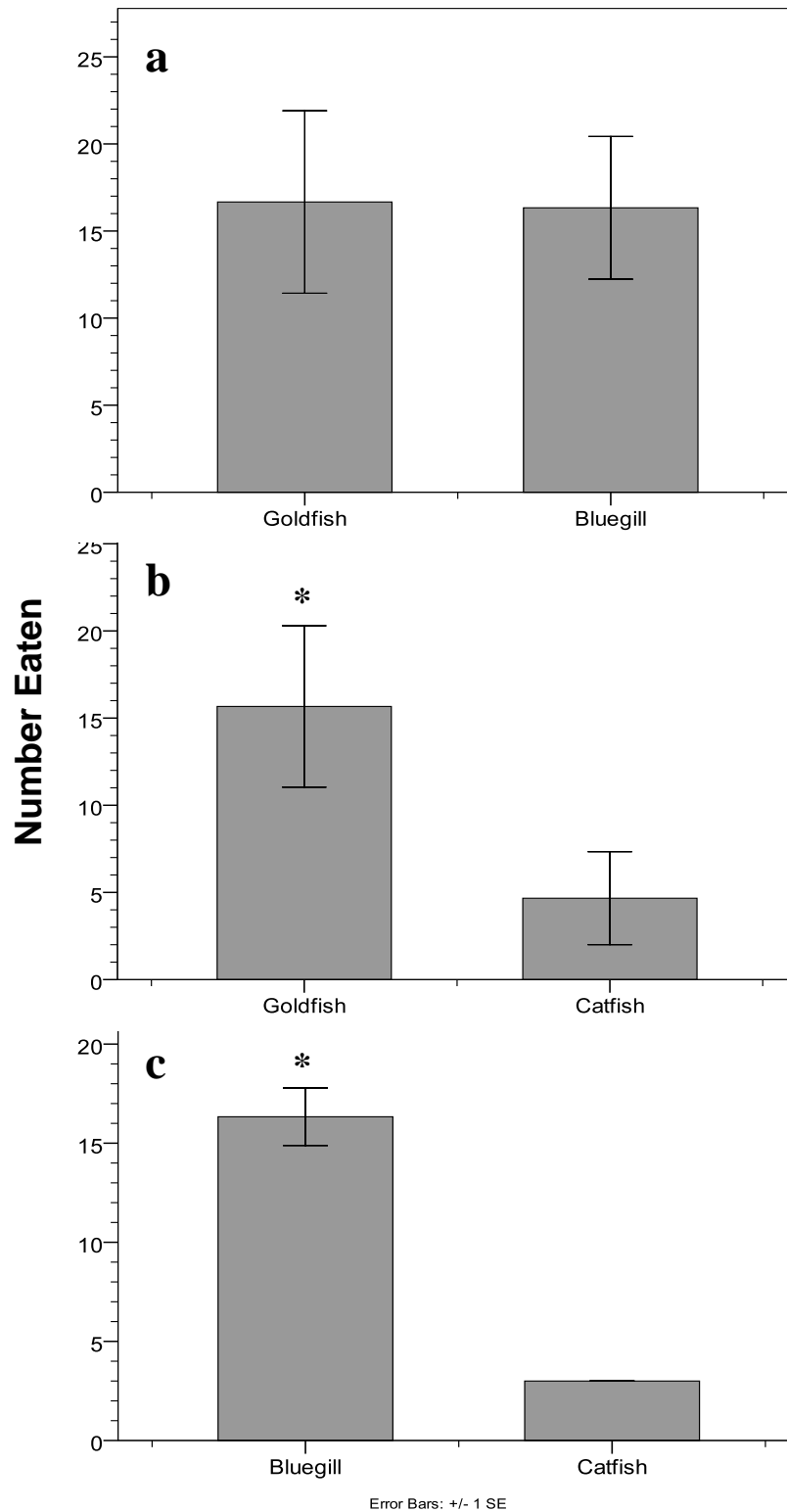
\*\* =  $p \leq 0.01$ , \*\*\* =  $p \leq 0.001$

**Figure 9.** Distribution of sizes of prey eaten versus not eaten for the first trial for pens stocked with 30 catfish (A) and 30 bluegill (B) (choice), (C) pens stocked with 60 catfish (non-choice) and (D) pens stocked with 60 bluegill (non-choice).



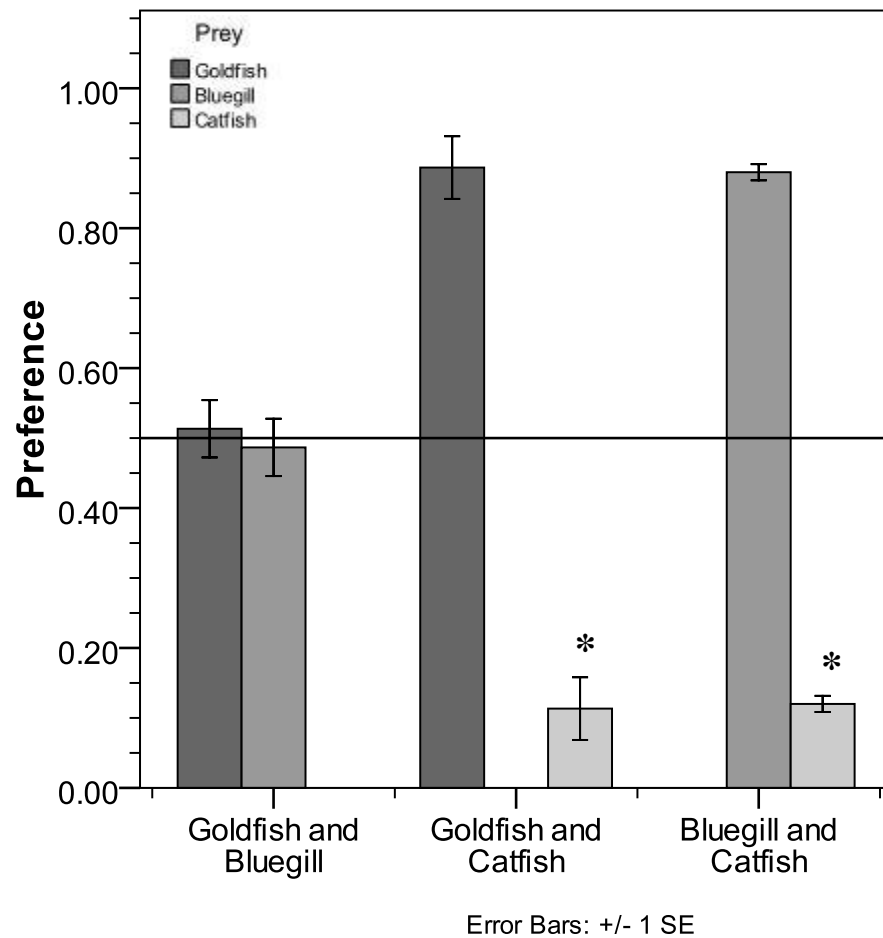
**Figure 10.** (A) Maximum TL, (B) mean TL and (C) mean weight of bluegill and channel catfish eaten in trial one per largemouth bass TL.





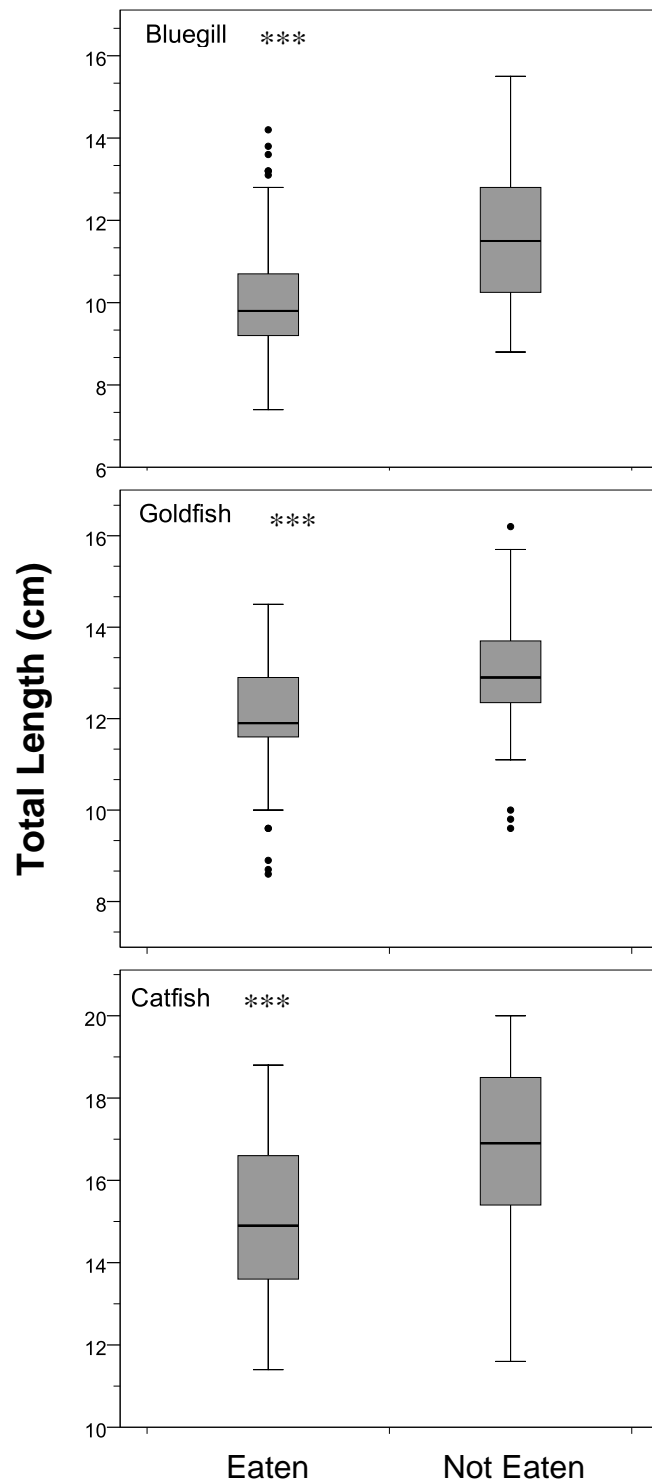
\* =  $p \leq 0.05$

**Figure 11.** The mean number of prey eaten by largemouth bass in the second net pen trial for pens stocked with (A) goldfish and bluegill, (B) goldfish and catfish, and (C) bluegill and catfish.



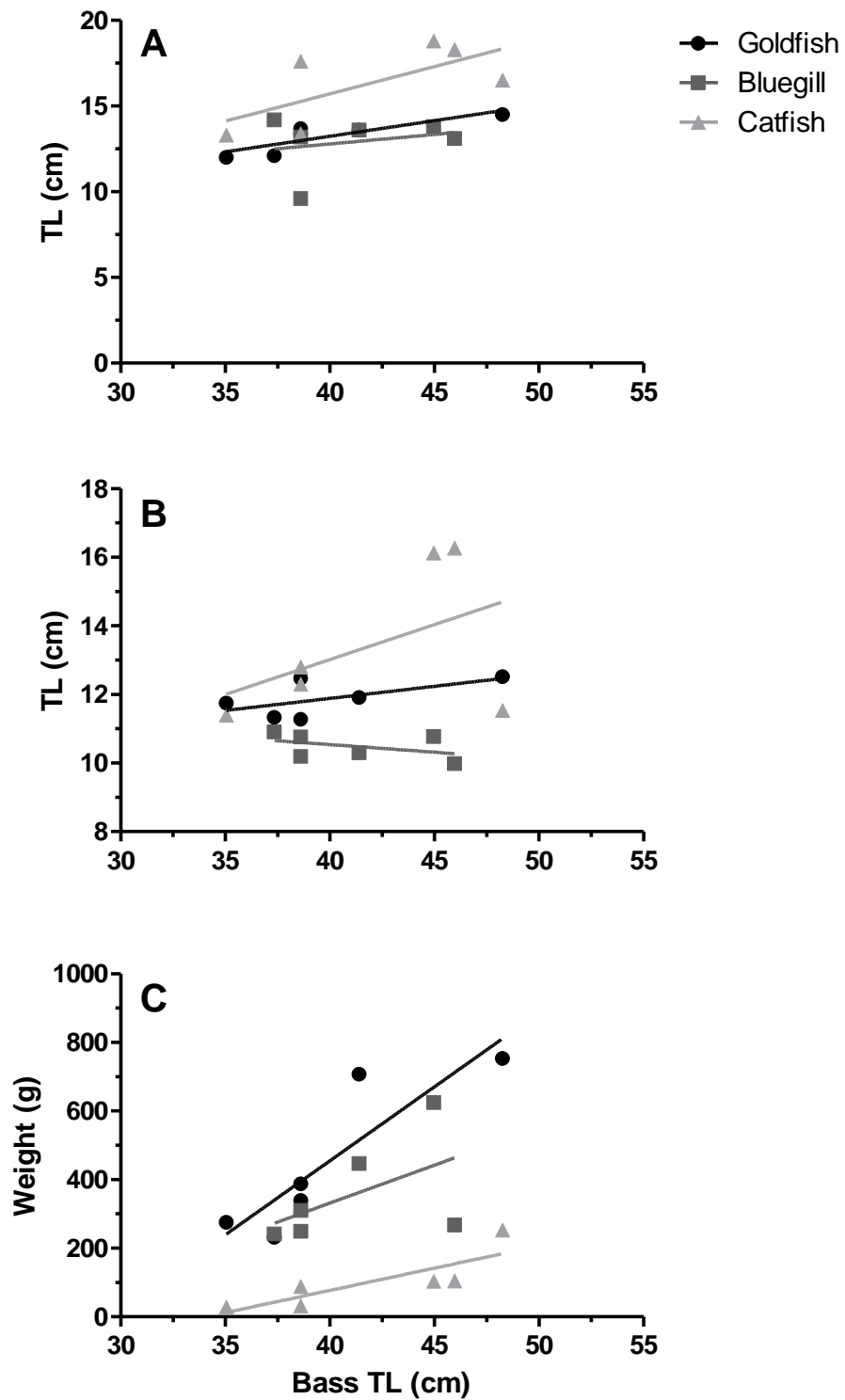
\* =  $p \leq 0.05$

**Figure 12.** Manly's  $\alpha$  values calculated for the second net pen trial during which bass were presented with combinations of two prey; including goldfish, bluegill, and channel catfish. The reference line indicates the expected preference of 50% for each prey.

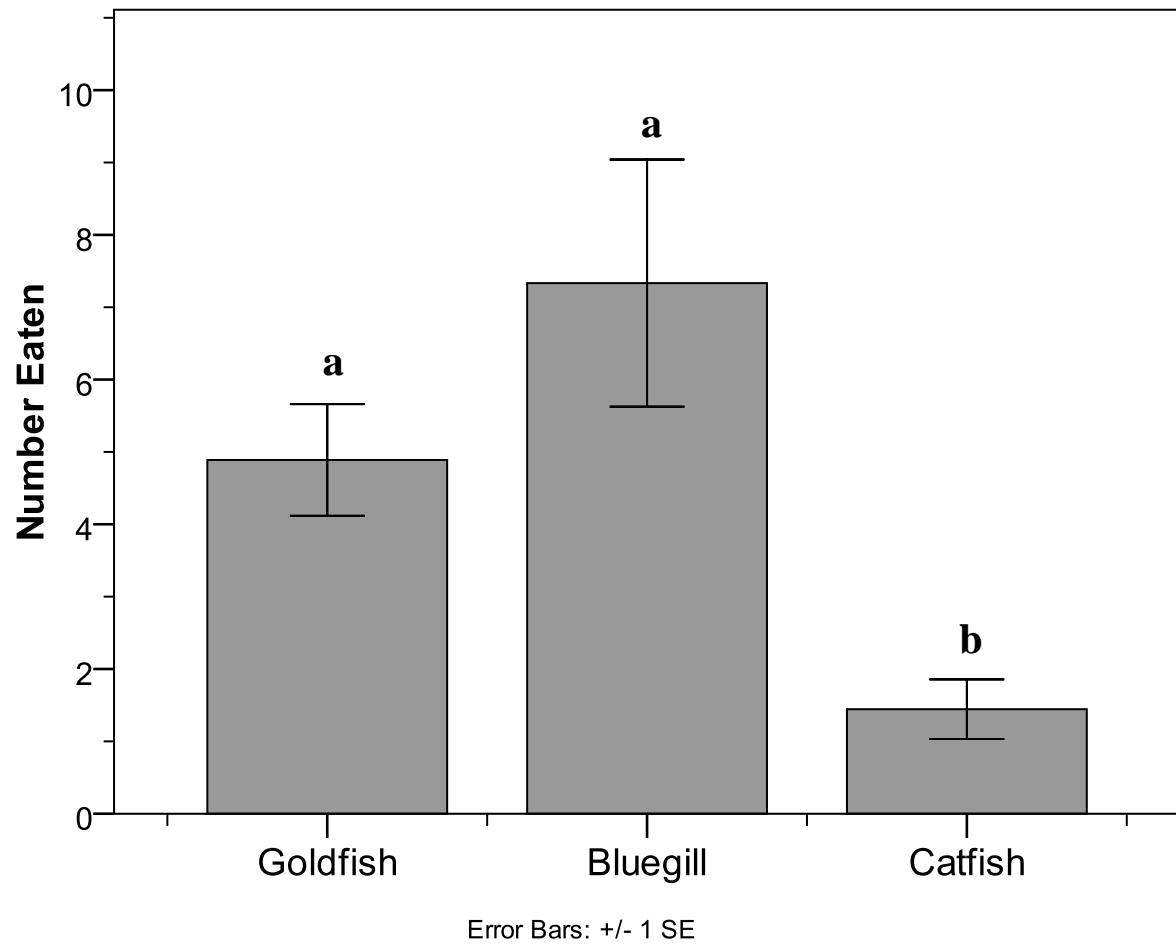


\*\*\* =  $p \leq 0.001$

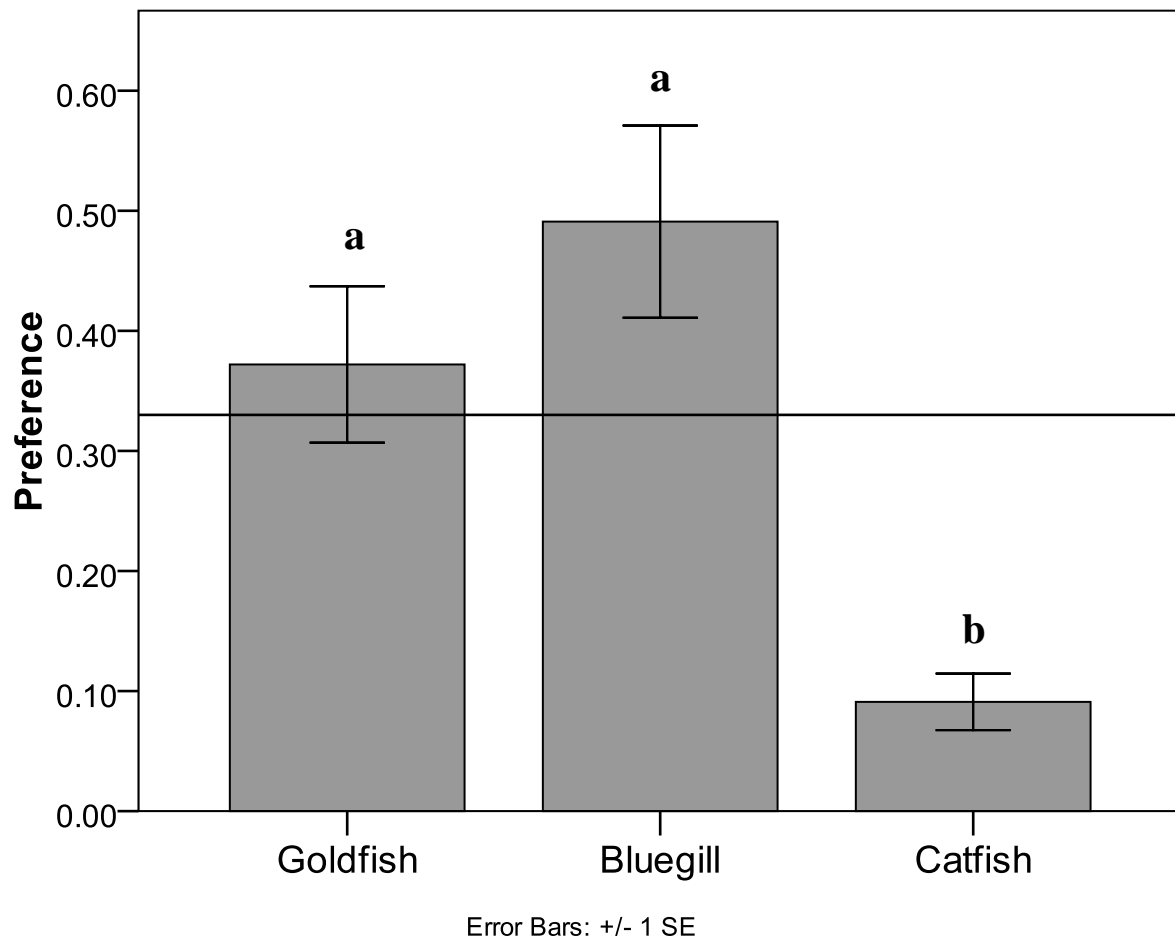
**Figure 13.** Size distribution (total length in cm) of goldfish, bluegill, and channel catfish eaten and not eaten by all largemouth bass for the second net pen trial.



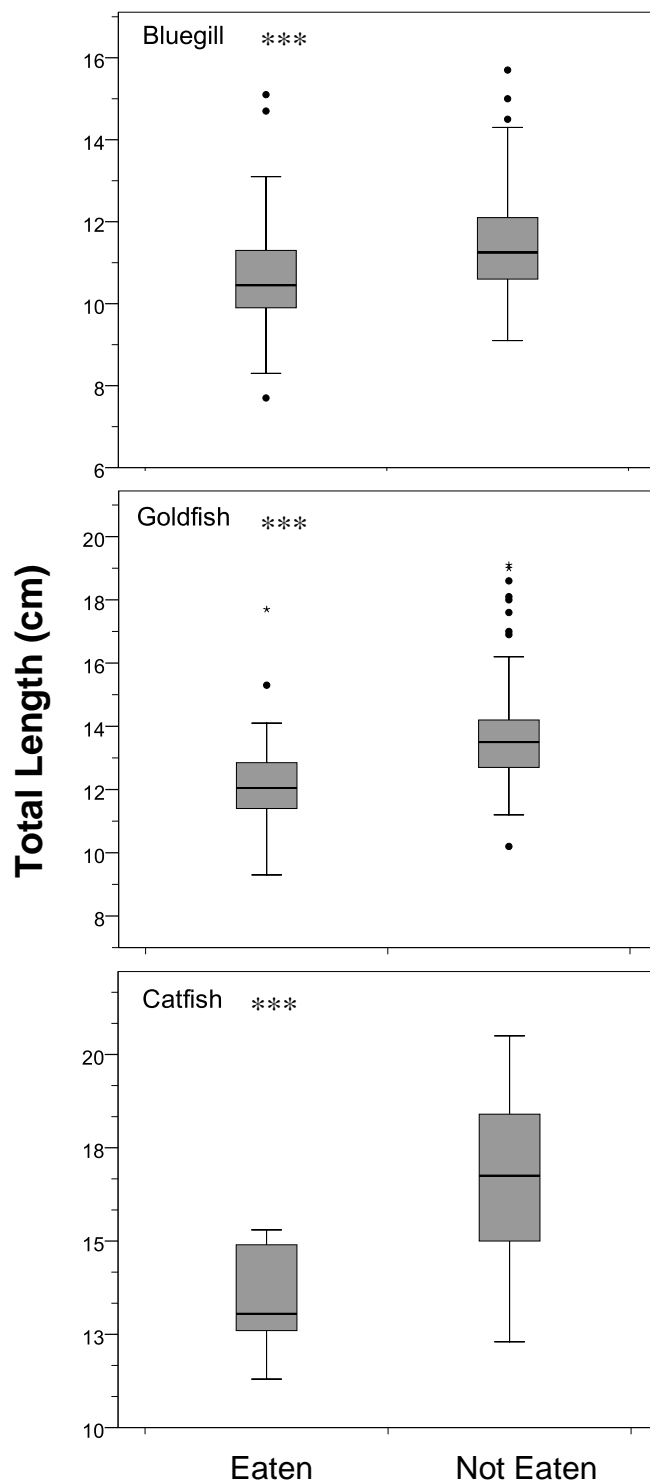
**Figure 14.** (A) Maximum TL, (B) mean TL and (C) mean weight of goldfish, bluegill, and channel catfish eaten in trial two per largemouth bass TL.



**Figure 15.** Mean numbers of goldfish, bluegill, and channel catfish eaten by largemouth bass in the third net pen trial.

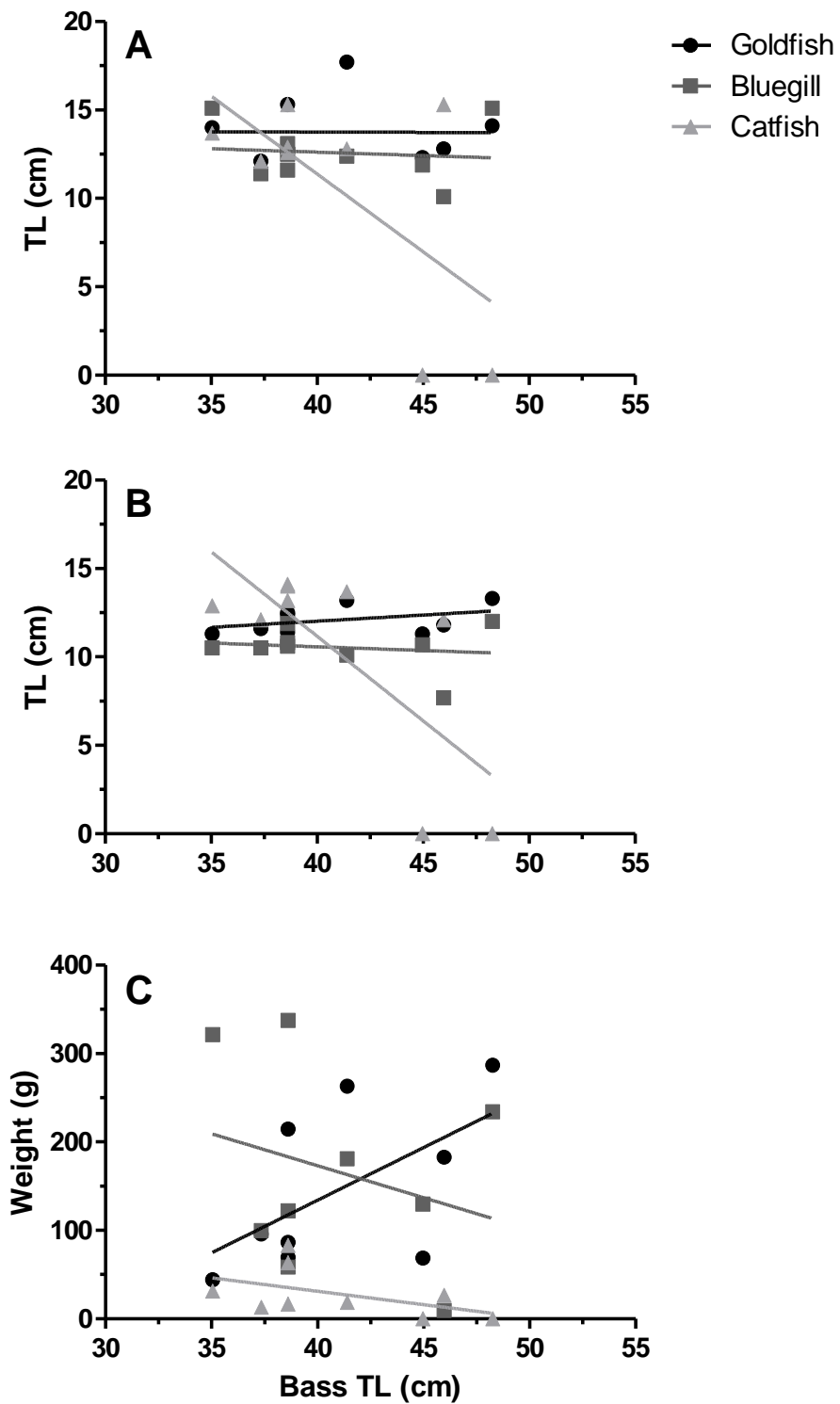


**Figure 16.** Mean Manly's  $\alpha$  values calculated for the third net pen trial during which all largemouth bass were presented with goldfish, bluegill, and channel catfish. The reference line indicates the expected preference of each prey of 33%.



\*\*\* =  $p \leq 0.001$

**Figure 17.** Size distributions (total length in cm) of goldfish, bluegill, and channel catfish eaten and not eaten for all largemouth bass in the third net pen trial.



**Figure 18.** (A) Maximum TL, (B) mean TL and (C) mean weight of goldfish, bluegill, and channel catfish eaten in the third net pen trial per largemouth bass TL.



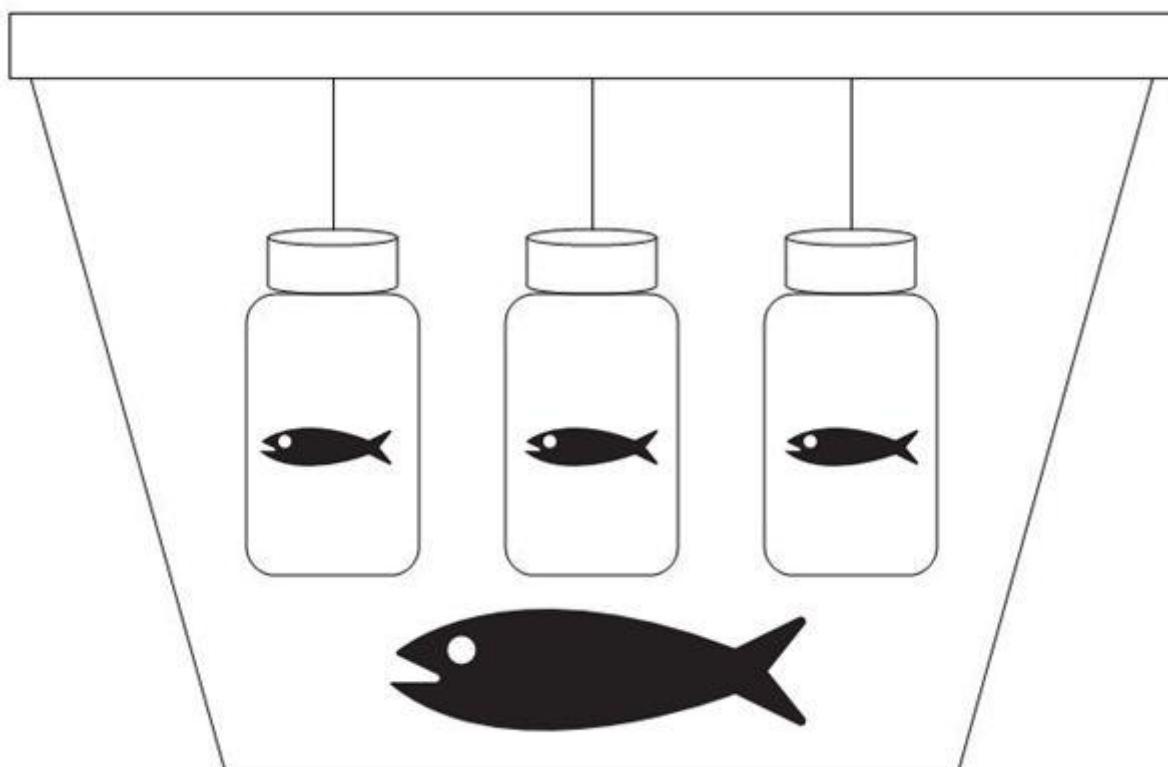
## REFERENCES

- Abrams, P.A. (1984). Foraging time optimization and interactions in food webs. *The American Naturalist* 124: 80-96.
- Bonar, S.A., J. Pahutski, B.D. Bolding, D. Fletcher, and M. Divens (1997). Survival and growth of channel catfish stocked in Washington lakes. *North American Journal of Fisheries Management* 17: 773-778.
- Borcherding, J. and C. Magnhagen (2007). Food abundance affects both morphology and behavior of juvenile perch. *Ecology of Freshwater Fish* 17: 207-218.
- Bosher, B.T., S.H. Newton, and M.L. Fine (2006). The spines of the channel catfish, *Ictalurus punctatus*, as an anti-predator adaptation: an experimental study. *Ethology* 112: 188-195.
- Britson, C.A. (1998). Predatory responses of largemouth bass (*Micropterus salmoides*) to conspicuous and cryptic hatchling turtles: a comparative experiment. *Copeia* 1998: 383-390.
- Brönmark, C. and J.G. Miner (1992). Predator-induced phenotypical change in body morphology in crucian carp. *Science* 258: 1348-1350.
- Brönmark, C., L.B. Pettersson, and P.A. Nilsson (1999). Predator-induced defense in crucian carp. In *The Ecology and Evolution of Inducible Defenses* (ed. R. Tollrian and C.D. Harvell), pp. 203-217. Princeton University Press, New Jersey.
- Brown, G.E. (2003). Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish and Fisheries* 4: 227-234.
- Bunkley-Williams, L., C. Allaume, T.N. Churchill, I. Corujo-Flores, C.G. Lilystrom, E.H. Williams, and A.J. Zerbias (1994). The South American sailfin armored catfish, *Liposarcus multiradiatus* (Hancock), a new exotic established in Puerto Rican fresh waters. *Caribbean Journal of Science* 30: 90-94.
- Burr, B.M. and J.N. Stoeckel (1999). The natural history of madtoms (genus *Noturus*), North America's diminutive catfishes. *American Fisheries Society Symposium* 24: 51-101.

- Chick, J.H. and C.C. McIvor (1997). Habitat selection by three littoral zone fishes: effects of predation pressure, plant density and macrophyte type. *Ecology of Freshwater Fish* 6: 27-35.
- Creel, S., D. Christianson, S. Liley, and J.A. Winnie Jr. (2008). Predation risk affects reproductive physiology and demography of elk. *Science* 315: 960.
- Dudash, M. and R.C. Heidinger (1996). Comparative survival and growth of various size channel catfish stocked into a lake containing largemouth bass. *Transactions of the Illinois State Academy of Sciences* 89: 105-111.
- Duvall, A. D. (2007). A comparison of the pectoral spines in Virginia catfishes. Masters Thesis, Virginia Commonwealth University.
- Emmett, B. and P.A. Cochran (2010). The response of a piscivore (*Micropterus salmoides*) to a venomous prey species (*Noturus gyrinus*). *Journal of Freshwater Ecology*; in press.
- Fine, M.L., J.P. Friel, D. McElroy, C.B. King, K.E. Loesser, and S. Netwon (1997). Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus*. *Copeia* 1997: 777-790.
- Forbes, S. (1989). Prey defences and predator handling behavior: the dangerous prey hypothesis. *OIKOS* 55: 155-158.
- García-Berthou, E. (2002). Ontogenetic diet shifts and interrupted piscivory in introduced largemouth bass (*Micropterus salmoides*). *Internat. Rev. Hydrobiol.* 87: 353-363.
- Gilliam, J.F., D.F. Fraser, and A.M. Sabat (1989). Strong effects of foraging minnows on a stream benthic invertebrate community. *Ecology* 70: 445-452.
- Glahn, J.F. and B. Dorr (2000). Captive great blue heron predation on farmed channel catfish fingerlings. *North American Journal of Aquaculture* 62: 149-156.
- Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385-398.
- Holt, D.E. and C.E. Johnston (2009). Signaling without the risk of illegitimate receivers: do predators respond to the acoustic signals of *Cyprinella* (Cyprinidae)? *Environ Biol Fish* 84: 347-357.
- Hoogland, R., D. Morris, and N. Tinbergen (1956). The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defense against predators (*Perca* and *Esox*). *Behaviour* 10: 205-236.
- Howick, G.L. and W.J. O'Brien (1983). Piscivorous feeding behavior of largemouth bass: an experimental analysis. *Transactions of the American Fisheries Society* 112: 508-516.

- Huntingford, F. and S. Coyle (2007). Antipredator defences in sticklebacks: trade-offs, risk sensitivity, and behavioural syndromes. In *Biology of the Three-Spined Stickleback* (ed. S. Östlund-Nilsson, I. Mayer, and F.A. Huntingford), pp. 127-156. Taylor and Francis Group, LLC, Boca Raton, FL.
- Jayne, B.C., A.F. Lozada, and G.V. Lauder (1996). Function of the dorsal fin in bluegill sunfish: motor patterns during four distinct locomotor behaviors. *Journal of Morphology* 228: 307-326.
- Jeffries, M. (1988). Individual vulnerability to predation: the effect of alternative prey types. *Freshwater Biology* 19: 49-56.
- Jenkins, R.E. and N.M. Burkhead (1994). *Freshwater Fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.
- Johnston, I.A. and J. Dunn (1987). Temperature acclimation and metabolism in ectotherms with particular reference to teleost fish. In *Temperature and Animal Cells* (ed. K. Bowler and B. J. Fuller), pp. 67-93. Cambridge: Society for Experimental Biology.
- Katano, O., T. Nakamura, and S. Yamamoto (2005). Prey fish selection by Far Eastern catfish *Silurus asotus* and largemouth bass *Micropterus salmoides*. *Fisheries Science* 71: 862-868.
- Kekäläinen, J., J. Kähkönen, V. Kiviniemi, and H. Huuskonen (2010). Morphological variation of perch *Perca fluviatilis* in humic lakes: the effect of predator density, competition and prey abundance. *Journal of Fish Biology* 76: 787-799.
- Kelley, J. L. and A.E. Magurran (2006). Learned defences and counterdefences in predator-prey interactions. In *Fish Cognition and Behavior* (ed. C. Brown, K. Laland and J. Krause), pp. 28-48. Oxford, UK: Blackwell Publishing Ltd.
- Krebs, C.J. (1989). *Ecological Methodology*. Harper Row Publishers, New York.
- Krummrich, J.T. and R.C. Heidinger (1973). Vulnerability of channel catfish to largemouth bass predation. *The Progressive Fish-Culturist* 35: 173-175.
- Lima, S.L. and L.M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Mittelbach, G. (1986). Predator-mediated habitat use: some consequences for species interactions. *Environmental Biology of Fishes* 16: 159-169.
- Moody, R.C., J.M. Helland, and R.A. Stein (1983). Escape tactics used by bluegills and fathead minnows to avoid predation by tiger muskellunge. *Env. Biol. Fish.* 8: 61-65.

- Nyberg, D.W. (1971). Prey capture in the largemouth bass. *American Midland Naturalist* 86: 128-144.
- Pimental, R., R.V. Bulkley, and H.M. Tyus (1985). Choking of Colorado squawfish, *Ptychocheilus lucius* (Cyprinidae), on channel catfish *Ictalurus punctatus* (Ictaluridae), as a cause of mortality. *Southwestern Naturalist* 30: 154-158.
- Robinson, B.W., A.J. Januszkiewicz, and J.C. Koblitz (2008). Survival benefits and divergence of predator-induced behavior between pumpkinseed sunfish ecomorphs. *Behavioral Ecology* 19: 263-271.
- Ryden, D.W. and J.R. Smith (2002). Colorado pikeminnow with a channel catfish lodged in its throat in the San Juan River, Utah. *Southwestern Naturalist* 47: 92-94.
- Spinelli, A.J., B.G. Whiteside, and D.G. Huffman (1985). Aquarium studies on the evaluation of stocking various sizes of channel catfish with established largemouth bass. *North American Journal of Fisheries Management* 5: 138-145.
- Wahl, D.H. and R.A. Stein (1988). Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117: 142-152.
- Werner, E.E., J.F. Gilliam, D.J. Hall and G.G. Mittelbach (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.
- Werner, S.J., M.E. Tobin, and P.B. Fioranelli (2001). Great egret preference for catfish size classes. *Waterbirds* 24: 381-385.
- Wisenden, B.D. and K.R. Harter (2001). Motion, not shape, facilitates association of predation risk with novel objects by fathead minnows (*Pimephales promelas*). *Ethology* 107: 357-364.



**Appendix I.** Schematic showing arrangement of jars during the jar study.



**Appendix II.** Arrangement of tanks for feeding trials with pumping system into adjacent pond.

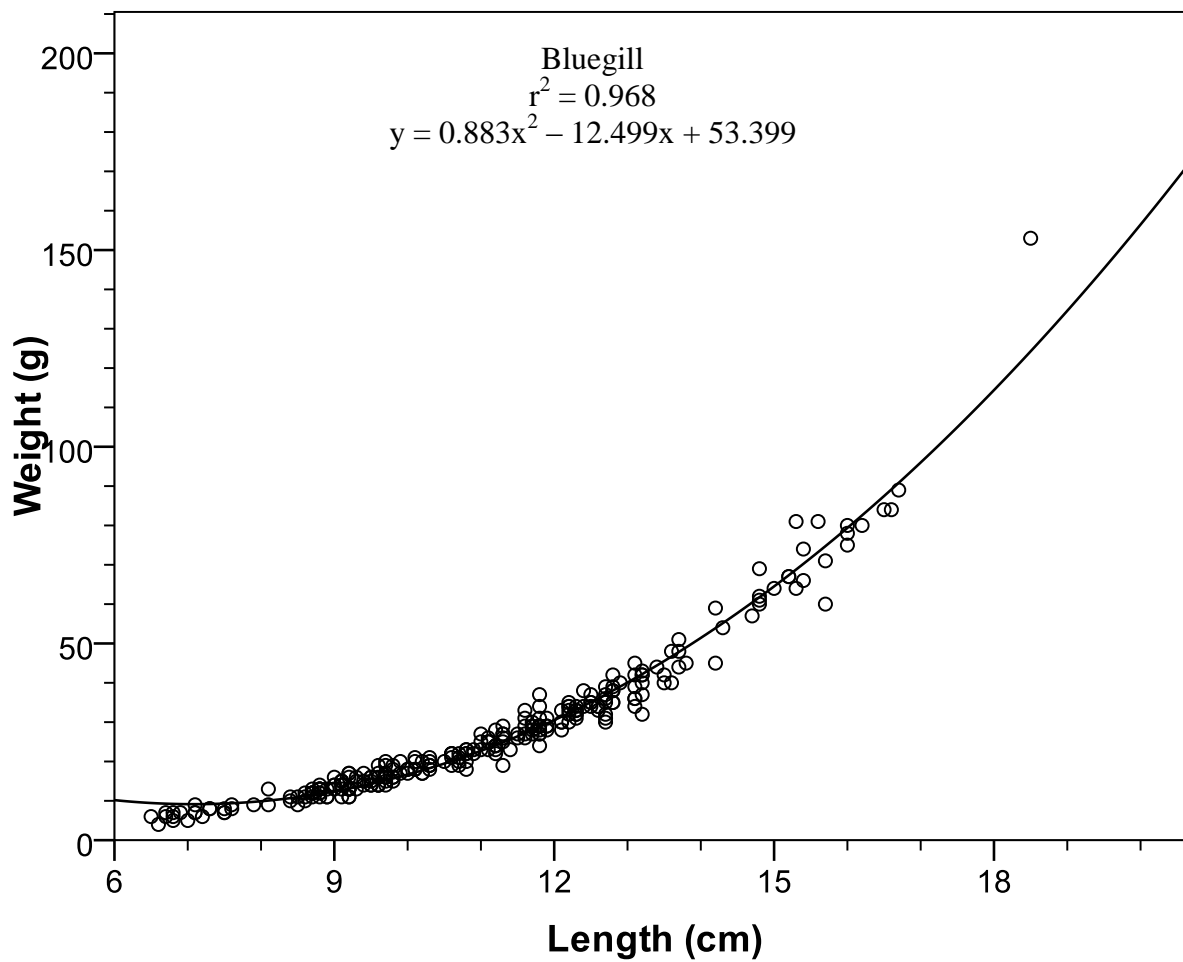


**Appendix III.** Shelter for bass constructed from peg board and PVC piping.

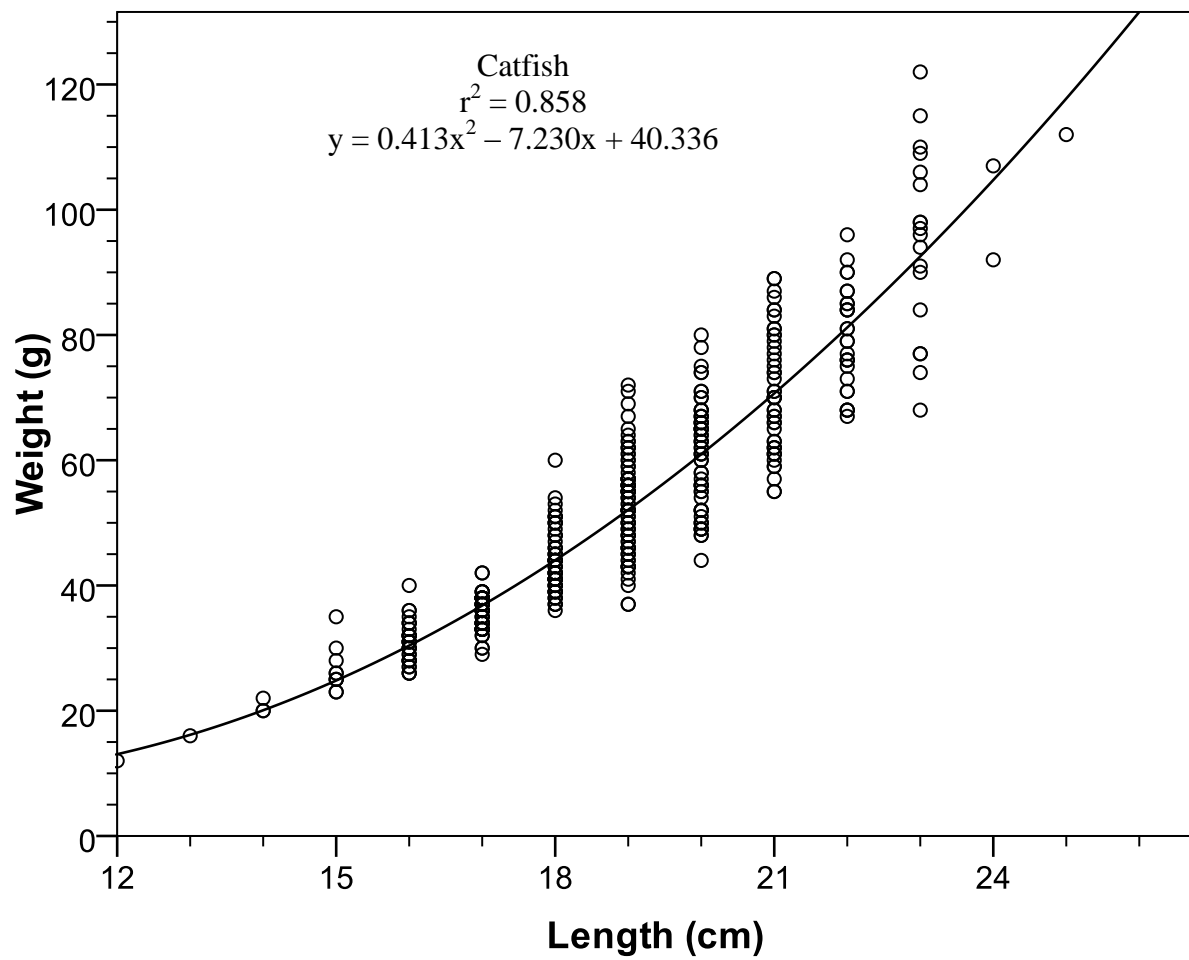


**Appendix IV.** Tank with mirror used to allow observation from a short distance to minimize stress on the bass.

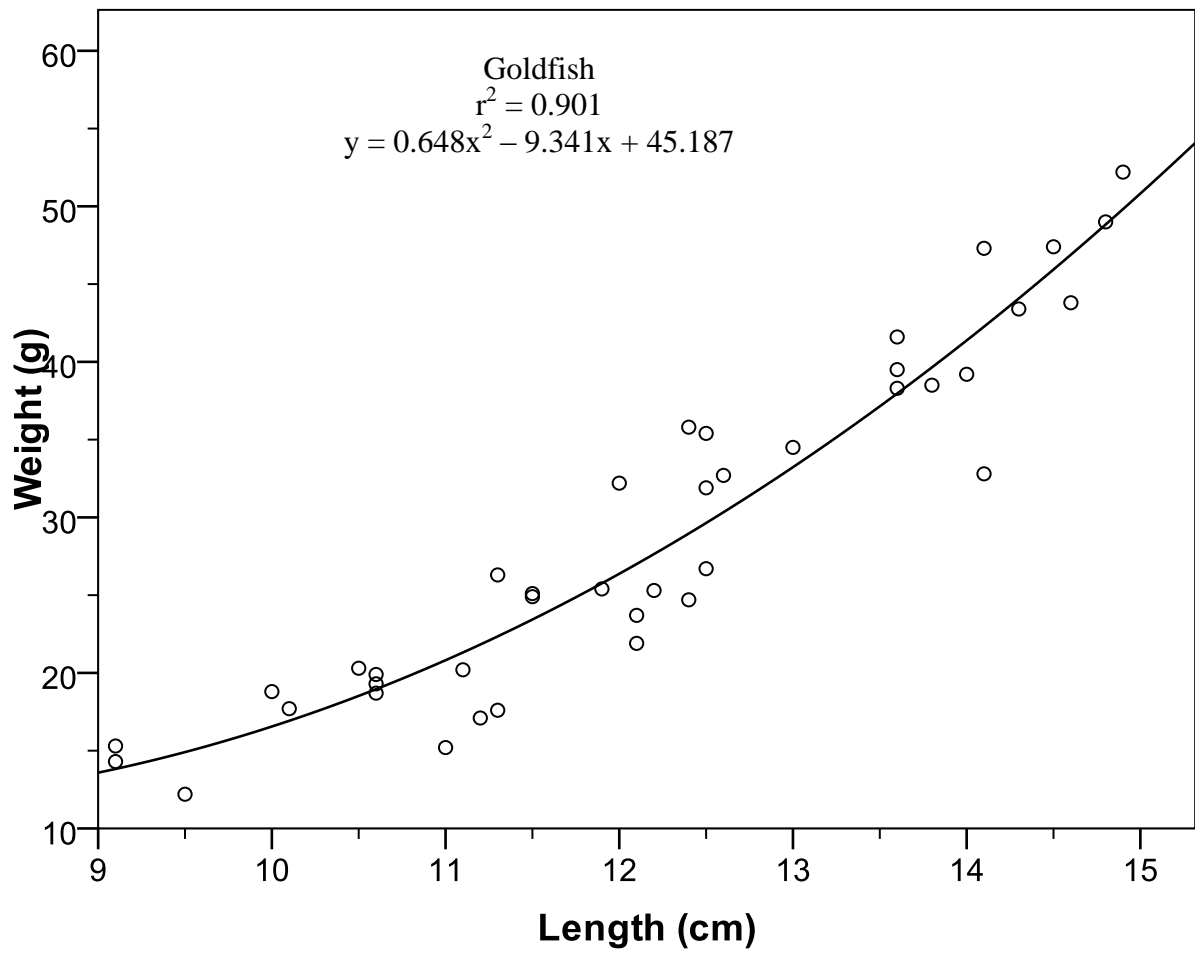




**Appendix V.** Length/weight regression for bluegill; data collected by Jonathan Harris at Virginia Department of Game and Inland Fisheries.



**Appendix VI.** Length/weight regression for channel catfish collected from aquaculture ponds at Virginia State University. The fish were purchased from a commercial supplier in Arkansas



**Appendix VII.** Length/weight regression for goldfish measured from aquaculture-raised stocks.

## VITA

Shelley Christine Nellis was born on June 11<sup>th</sup>, 1986 in Virginia Beach, Virginia, U.S.A. She graduated from Powhatan High School in 2004, and received a Bachelor of Science in Biology from Virginia Commonwealth University in 2008. She began the Master of Science in Biology program at VCU in the Fall of 2008.